NATURAL SELECTION RECONSIDERED

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PREFACE

This thesis is the result of my own work and includes nothing which is the outcome of work done in collaboration except as declared in the Preface and specified in the text. It is not substantially the same as any that I have submitted, or, is being concurrently submitted for a degree, diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text. I further state that no substantial part of my dissertation has already been submitted, or, is being concurrently submitted for any such degree, diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text. This thesis does not exceed the prescribed word limit does not exceed the word limit prescribed by the Department of History and Philosophy of Science Degree Committee.

ABSTRACT

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In this thesis, I inspect some key assumptions which tend to underpin mainstream accounts of natural selection, noting where those assumptions break down and taking this as a basis for fresh analysis.

First, I examine the assumption that natural selection inherently involves struggle or competition. I show selection can take place without zero-sum competition and that competition is not essential for selection to positively facilitate novel adaptations.

Moving on to fitness, I address the assumption that biological fitness should be measured as a function of the number of elements of some set of entities (offspring, gene copies or otherwise). Noting cases where selection seemingly acts in terms of persistence and somatic growth, and with these alternative fitness metrics not reducible to one another, I suggest a pluralist stance. Subsequently extending this rationale to the temporal dimension, I show that attempting to measure fitness over any single time frame often fails to capture the action of selection.

In later chapters, I explore the possibility of uniting my multiple fitness metrics via a single "common currency" metric. I rule out metrics based around resource or energy consumption, as per Van Valen and others, as unworkable. However, I find some potential in conceptualising the various aspects of fitness in terms of negative entropy. This fails to deliver a quantifiable common currency metric, but does address conceptual issues and allows for the unification of our account of biological fitness with the popular thermodynamic definition of life.

The need to buttress earlier arguments necessitates a concluding analysis of the Darwinian population concept. Contra complacent assumptions that they are readily defined, I find that there are no clear means to bound Darwinian populations in many cases. I also argue that analysis of the Darwinian population concept has been confounded by the conflation of pragmatic groupings, assembled for comparative inference, with causally bound Darwinian populations.

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Otherwise, I had previously grouped long and personal acknowledgements with overly gushy award speeches; as something to eschew in the name of good taste. However, recent years have certainly not gone by without any hitches and, as it turns out, I find myself hugely indebted to more people than I can realistically credit here. These wonderful individuals will know who they are and I hope that, by mentioning only a subset here, I do not do the remainder an unforgivable disservice.

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INTRODUCTION

Any student of evolution will be aware of the fierce and ongoing debates surrounding all the major elements of our theory of natural selection. Philosophers and biologists have built up the literatures concerning the most frequently revisited questions to formidable size, with burgeoning corpora of work on issues such as the appropriate level of organisation to locate units of selection and how to properly understand biological fitness (reviewed respectively in Rosenberg and Bouchard 2015 and Lloyd 2020).

However, despite all this disagreement, it is also true that even the most novel contributions to these debates will generally begin from a shared, underlying consensus on the fundamental character of natural selection. Whilst authors might disagree on the details as to how to elaborate our theory of natural selection, they will generally hold a certain set of basic commitments in common.

We might think that such foundational consensus is to be expected from any mature field of study – that our basic theoretical commitments should be established beyond reproach and that subsequent research will focus on the details of interpretation and implementation (we might think of this as part of something like Kuhnian "normal science" – as per Kuhn 1962). In this piece, though, I will make it my task to investigate the extent to which this underlying consensus is actually established and defensible. I will show that multiple assumptions underpinning the conventional understanding of natural selection do not, in fact, stand up to scrutiny. Generally, I argue that selection exists as a rather broader phenomenon than our present accounts are capable of capturing.

My concern here is not simply to demonstrate problems for our received view of selection but also to offer solutions or reformulations designed to rectify theory where possible. My recommendations, by accounting for the realisation that selection functions in more modes than our current characterisation allows for, will offer significant increase in explanatory scope for our theory of natural selection. It will become apparent that the received view of natural selection can, at best, be thought of as a specific case of a more general phenomenon. Thus, our standard assumptions constrain our theory of natural selection to dealing with only a subset of valid cases of selection. Existing accounts are shown to be appropriate for dealing with selection in the most "familiar" species, but rapidly break down as we move towards other selective scenarios.

Before diving into analysis, I will use this introduction to address a few questions which emerge at this point. Specifically, I will deal with the following:

1. To what do I take the term "natural selection" to refer?

I clarify the target of my analysis.

2. Which specific assumptions are to be tackled?

After taking examples from literature, I enumerate the precise assumptions I will be examining.

3. How will I go about this?

I provide a chapter-by-chapter breakdown of my upcoming analysis.

4. Why bother?

I explain why we might think this is a worthwhile project to embark upon at all.

Of course, our understanding of all of these issues will become more nuanced over the course of the discussion. Thus, after dealing with these initial clarificatory points, I will move directly on to commence analysis in chapter one.

1. To what do I take the term "natural selection" to refer?

The term natural selection is given multiple meanings across both popular and academic discussion (Gildenhuys 2019). On the most naïve consideration (though also with some theoreticians), natural selection is equated with adaptive evolution. Thus, if a layperson were offering an explanation of how it was that *Homo sapiens* emerged from a hominid ancestor, they might be just as likely to state that this was due to "natural selection" as "evolution", using the two terms interchangeably. However, most specialists would not endorse this kind of usage and would point out that natural selection is only one factor in the evolution that allows us to explain the emergence of *Homo sapiens* and other new forms.

Indeed, the term "evolution" itself can be ambiguous and is frequently used in two senses that we might loosely characterise here as "creative" and "populational". Thus, the advent of each of the new adaptations that punctuate the journey from primate ancestor to modern human – for example, increase in brain size providing enhanced cognitive capacity and alteration to bone structure permitting bipedal locomotion – would be instances of "creative" evolution, referring to the genesis of novel adaptive traits. This is evolution in the sense generally used by the layperson.

However, in a slightly more technical sense, we can also describe the more immediate population dynamics between existing variants as constituting evolution. Thus, what we might call "populational" evolution occurs simply when the frequency of different types in a population changes over time, without the emergence of any novel traits. For example, if we see some pathogen wipe out one variant within a population, we can say that the population has evolved in the populational sense here, even though there has been no emergence of new forms.

Populational evolution will occur as the combined result of both random drift and natural selection as I will consider it here. For instance, changes in relative numbers of two variants in a population might be explained by reference to the systematic result of natural selection and/or the effect of random factors associated with drift. Particularly where creative evolution gives rise to the kind of complex novel traits that mark out homo sapiens from its predecessors, these adaptations will typically then be explained as the result of multiple iterations of such populational evolutionary change, with the input of novelty via mutation.

Natural selection, as I refer to it here, then, is far from synonymous with evolution, however one uses that term. Rather, in summary, natural selection combines with drift to generate populational evolution. The iterating action of populational evolution, with mutation, can then generate creative evolutionary change whereby complex new adaptive forms may emerge. Of course, this is hardly an innovative picture and will likely all seem very obvious to many readers.

However, it is not only laypersons that tend to make equivalencies between natural selection and "creative" evolution, as I have called it. A major reason for my having to include these clarificatory remarks is the fact that some theoreticians would limit consideration of natural selection in its "truest" form to instances of population dynamics that give rise, or are likely to give rise to, novel adaptive traits. For example, Godfrey-Smith (2009) defines "paradigm" instances of natural selection as those likely to lead to such new adaptations (thus allowing for natural selection to be invoked in what Godfrey-Smith calls "origin explanations" – discussed in detail in chapter one).

I will argue against the coherence of placing these kinds of constraints on our concept of natural selection. Of course, though, how we choose to employ the term "natural selection" will ultimately be a matter of taste as much as anything else. Here, it is enough to indicate how I will use the term natural selection throughout this piece, so as to avoid confusion with those who prefer a different usage.

2. Which specific assumptions are to be tackled?

Our schematic statements of the basic requirements for, or fundamental nature of, natural selection are separable from how we then elaborate and apply our accounts of that phenomenon. That being said, such statements do serve to indicate the assumptions built into the foundations of conventional theories of natural selection.

To this end, we can sample a few such descriptions of natural selection as a means to identify those assumptions that tend to recur in our thinking about selection more generally. Here, I will present a transect of descriptions, ranging from the "popular" through to the more technical. Many other examples are available, but only a few are required to make my point, as the same basic assumptions come up again and again, right across the spectrum from popular to technical resources.

Let us begin from our most "popular" source. If a layperson wanted to define the term natural selection, they might turn to a source like the *Encyclopaedia Britannica*:

> In natural selection, those variations in the genotype (the entire complex of genes inherited from both parents) that increase an organism's chances of survival and procreation are preserved and multiplied from generation to generation at the expense of less advantageous variations. Evolution often occurs as a consequence of this process. Natural selection may arise from differences in survival, in fertility, in rate of development, in mating success, or in any other aspect of the life cycle. All such differences result in natural selection to the extent that they affect the number of progeny an organism leaves. (Editors of Encyclopaedia Britannica 2020)

Referring to a respected undergraduate-level textbook, we find the following definition in Ridley's *Evolution*. After a discussion of competitive struggle in the natural world, Ridley gives us the following schematic statement of the criteria required for natural selection to operate. As I will note again in chapter one, this is a version of the well-known Heritable Variation of Fitness (HVF) criteria from Lewontin (1970:1), but with an appended specification of the need for competition:

> The excess fecundity and consequent competition to survive in every species provide the preconditions for the process Darwin called natural selection. Natural selection is easiest to understand, in the abstract, as a logical argument, leading from premises to conclusion. The argument, in its most general form, requires four conditions:

> 1. Reproduction. Entities must reproduce to form a new generation.
> 2. Heredity. The offspring must tend to resemble their parents: roughly speaking, like must produce like"
> 3. Variation in individual characters in the members of the population. If we are studying natural selection on body size, then different individuals in the population must have different body sizes […]
> 4. Variation in the fitness of organisms according to the state they have for a heritable character. In evolutionary theory, fitness is a technical term meaning the average number of offspring left by an individual relative to the number of offspring left by an average member of the population. This condition means that individuals in the population with some characters must be more likely to reproduce (i.e., have higher fitness) than others […] (Ridley 1996:71-72)

Much the same treatment is offered in a similarly widely read undergraduate textbook by Krebs and Davies (1981:9 – though the pair also add a statement of the same approach but in terms of gene frequencies), effectively presenting HVF criteria with the added requirement of resource competition. The authors provide a one-line summary of this definition as:

> Heritable variation with competition for survival and reproduction (Krebs and Davies 1981:9)

To take a sample from more specialist literature, within the philosophy of biology, Brandon's oft-cited Principle of Natural Selection (or PNS) provides a brief, precise description of selection as follows:

> For any two individuals, *x* and *y*, if *x* is fitter than *y* in environment *E*, then, probably, *x* will have more offspring than *y* in *E*. (Brandon 1990)

We could refer to any number of additional sources here. However, this handful of quotes, sampled across the spectrum from more popular to more technical sources, already help demonstrate how the same set of fundamental commitments recur in different combinations across conventional definitions of natural selection. In particular, across the subsequent chapters, I will be concerned with the following common underlying assumptions in how we consider natural selection:

> ***1. Competition is an inherent part of natural selection***
> It is common to hold that some form of competition, or the related notion of "struggle", is a prerequisite for natural selection to occur (Lennox and Wilson 1994, Glymour 1999 and Bernstein et al 1983 provide a good sample of requirements for various forms of struggle and/or competition). Even where a commitment to competition is not directly stated, it is frequently

implied by discussion of the success of some type being "at the expense of" another (as per our Encyclopaedia Britannica quote above) or even with the language of competitive exclusion; where we are given the idea that the success of one type will be accompanied by the "elimination" of another.

2. Assessing fitness is a matter of counting some number of units

There are disagreements over whether we should track biological success in terms of individual offspring, gene copies or perhaps trait tokens (Rosenberg 2002:§3). We might also disagree as to whether we want to measure fitness retrospectively, as an already-realised quantity, or as a propensity (as per Mills and Beatty 1979). Whichever of the mainstream views we subscribe to, though, fitness will generally be measured as a function of the number of whichever kind of biological individual in which we are interested. Thus, fitness measurement will be a matter of *counting elements* in a relevant set, whether we prefer to count organisms, gene copies or trait tokens. We can contrast this "numerosity approach" (as I will label it in chapter two) to the idea of assessing fitness in terms of total biomass or the persistence of individuals or lineages, where we are interested in quantities other than the number of elements in some set of entities. The resulting fitness values would, of course, still be *numerical* (presumably as some function of kilograms of biomass or duration in years), but would not be a function of the number of individual entities in some set - and so would be distinct from the typical "numerosity" approach.

3. Fitness is manifested in an immediate, single-generation time frame

Generally, biological success will be discussed in terms of contribution of offspring, gene-copies or otherwise *to the next generation*. The common assumption is that fitness should be measured, and that natural selection operates exclusively, over this time scale (discussed in Beatty and Finsen 1989 and Sober 2001). This will be contrasted to cases where selection seems to operate within multi-generational timescales.

4. The population involved in a case of natural selection is self-evident

Almost any description of natural selection seems to take for granted that we have already decided on which set of entities are being selected alongside one another. This is to say, we assume the "Darwinian population" is readily defined. None of the descriptions above give detailed guidance as to how we bound the relevant Darwinian population, and this reflects the rarity with which the issue is discussed in the literature more generally. This omission has also been noted by Stegenga (2016) and Millstein (2009), who draws attention to resulting confusion caused for biologists. More specifically, there is a further general assumption (dealt with in

chapter six) that the Darwinian population will be defined via some causal connection between members that is relevant to the outcome of selection.

Not all authors will explicitly commit themselves to all of these assumptions at once. For instance, we have seen that Lewontin develops a widely cited conventional account but does not require competition for selection (something Lewontin himself states explicitly, and to which we will return in chapter one). By contrast, the account from Bernstein and collaborators (Bernstein et al 1983) amounts to a largely similar view on selection, but with resource competition given an intrinsic role. With this said, someone holding to all these assumptions would position themselves at the very centre of mainstream thought on natural selection.

Now, some readers will correctly note that more abstract formulations of natural selection do not necessarily contain these assumptions. Lewontin's (1970:1) HVF criteria and especially the Price Equation (Price 1970, Gardner 2008) are sufficiently general to be applied to any number of biological and non-biological systems at any time scale. However, the fact remains that these ideas are still typically deployed in the context of the standard assumptions listed here.

As noted, Lewontin's HVF criteria themselves do not imply resource competition. However, those criteria are typically deployed alongside either implicit or explicit assumptions constraining their use to apparently competitive scenarios – as with Ridley and Krebs and Davies above. Similarly, Brandon's PNS as relayed here is compatible with multiple time periods at which to count offspring number. However, Brandon himself elsewhere (1990:24–5, also quoted in Sober 2001 and noted here in chapter three) defends the idea that selection operates in a short-term time frame only, and it seems this is how he meant the PNS to be interpreted. Thus, these assumptions need to be dealt with, whether or not we believe they are logically contained within the most general theoretical treatments of selection.

3. How will I go about this?

So far, I have said quite a bit about what I will be doing at a high level, but have been light on specifics. As such, it will be useful to run through a chapter-by-chapter overview as to precisely what ground I will cover. Across my six chapters, I will set out to tackle the four typical assumptions underlying conventional approaches to natural selection set out above, with these leading into further fundamental issues. In particular, examining the assumption that fitness is always a business of counting the number of some set of entities will lead to the knotty problem of how indeed we ought to denominate fitness if counting alone will not suffice.

I. Struggle, Competition and Natural Selection

In this opening chapter, I begin by examining the assumption (number one, above) that natural selection necessarily involves some element of struggle or, more commonly, competition. I note that, where they are discussed at all, struggle and competition have typically been identified with zero-sum competition and I further support the idea of zero-sum competition being the only coherent, objective means by which to translate these originally human notions into the natural world.

I identify several qualities making selection driven by zero-sum competition especially dynamic and powerful. However, I also note that the same or similar qualities will be instantiated in cases of selection driven by other forms of interaction between individuals – with my specifically identifying mutualistic and exploitative interactions. These forms of interaction are characterised via configurations of the alpha values associated with the Lotka-Volterra equations, which will be employed to structure discussion.

I also question the idea associated with Godfrey Smith (2009), that competition is a necessary feature of selection where it is to explain the emergence of novel adaptive traits (that is, to make Godfrey-Smith's "origin" explanations). Rather, I show that selection driven by mutualistic or exploitative interactions is arguably *better* suited to support such explanations. The only route I identify by which competitive instances of selection can explain the emergence of novel adaptive traits is also open to cases of selection where there are no salient causal interactions at all – that is, no zero-sum competition, no mutualism and no exploitation.

Summing up my findings, I propose a new taxonomy of modes of selection to replace that offered by Godfrey-Smith (2009). Thus, I borrow terminology from game theory to partition "parametric" and "strategic" forms of selection; further segmenting the latter category into competitive, cooperative and exploitative modes.

II. Fitness Metric Pluralism

This chapter is the first of an interrelated series of four, where I explore our concept of biological success in some depth. To begin, I examine the assumption that fitness should be measured as a function of counting the number of some set of entities – whether these be individual organisms, alleles or trait tokens. I group such conventional accounts of fitness together as "numerosity" approaches.

To facilitate discussion in this and subsequent chapters, I set out a tripartite distinction between fitness "metric", "measurement scheme" and "concept". These three categories can be thought of as different components that every complete account of fitness must contain, or as separate levels of analysis where we might engage with fitness.

In the main discussion, I demonstrate that there are many instances where a numerosity approach to fitness appears insufficient to capture the action of selection. I examine the various options for retaining something like a conventional approach to fitness. However, I show both that the various fitness metrics discussed fail to reduce to any one of their number and that limiting our account of fitness to any one of these metrics will inherently lead to the loss of biologically salient information – thus constraining our ability to make valid selective explanations. As such, I advocate for a pluralist account of fitness in this regard, also arguing that the conventional assumption that fitness must be a unidimensional phenomenon would need a positive justification, which has never been supplied. This conclusion is noted to be provisional, though, as it might be the case that all the metrics discussed can be reduced to some further, common currency metric outside the mainstream literature. Relatedly, I also note that a pluralist approach leaves us with conceptual questions as to the criteria distinguishing valid from invalid fitness metrics. I defer these issues for fuller discussion in chapters four and five.

III. Fitness and Time

Here, I temporarily leave aside direct discussion of fitness metrics to examine the assumption (number three, above) that biological fitness ought to be measured over a single-generation time frame. I begin by explaining that this assumption has received some attention in the literature already, with several well-known problems where conventional approaches to fitness de-link from biological success over time. I also differentiate the specific problem I will be concerned with from the widely cited issue around dealing with reproductive output over time associated with Gillespie (1977).

Shadowing the logic of chapter two, I find that insisting upon *any* single measure of fitness over time will lead to a loss of biologically salient information. As such, I recommend an "intra-case pluralist" approach to fitness measurement over time. I note that this approach means that we cannot always rank the fitness of types over all time. However, I show that it allows us to better understand how levels of biological success at different points in time can depend upon one another and how trade-offs between them might be selected for.

IV. Consumption Accounts of Fitness

Here, I return to the broad concerns of chapter two. In that chapter, I showed that the different putative fitness metrics we had encountered were not reducible to one another. However, I indicated that, whilst no candidates were available in the mainstream literature, it was notionally possible to find a "common currency" metric to render the various aspects of fitness commensurable. Relatedly, I noted that allowing for multiple fitness metrics leaves us with conceptual-level questions around what unites valid metrics and what allows us to exclude invalid ones.

In chapter four, then, I venture outside the mainstream literature to examine the possibility of conceiving of biological success as some function of energy or resource consumption. This would leverage the apparent truth that the processes associated with biological success are all inherently costly in terms of energy or resources, promising to reconcile the various aspects of fitness from chapter two with a common currency metric and a unifying fitness concept.

Thus, I examine Van Valen's (1973, 1975, 1976, 1989) work on selection and fitness as the most well-developed literature considering fitness in terms of both resource and energy consumption. The idea of reducing fitness to a readily measured, fundamental physical quantity like energy is appealing in itself. However, consumption accounts promise several significant advantages beyond this. Most salient is that having a common currency between the different aspects of fitness makes possible a whole host of fitness comparisons that are barred by conventional accounts. The result would be a huge increase in explanatory scope for our theory of natural selection.

With Van Valen's account as an example, I note various fundamental problems for consumption approaches in general. In particular, I show that Van Valen's or any similar consumption account will be vulnerable to "efficiency" problems, where input of energy or resources will not track output in terms of biological success. I also point to cases of what seem like clear instances of selection, but involving non-metabolic entities, which do not engage in the consumption of energy and/or resources at all.

Van Valen's work is particularly useful in having anticipated some of these issues and proposed solutions. However, I show that these responses are insufficient to solve the problems they purport to address. Thus, I ultimately reject consumption accounts of fitness as unworkable.

V. A Thermodynamic Approach to Fitness

Whilst consumption accounts are not feasible, they promise great increases in explanatory scope for our theory of natural selection and appear to get at something valid with their analysis in terms of underlying physics. In this chapter, then, I attempt to develop an approach that might capture these advantages without inheriting the problems associated with consumption accounts.

To begin, I return to first principles to consider what the different aspects of biological success identified in chapter one have in common and what it was that consumption accounts seemed to capture so well. Doing so, I note significant parallels between what we have said about fitness and Schrödinger's (1944) well-known definition of life as the maintaining or increasing of "order" or negative entropy in the face of the general decay predicted by the second law of thermodynamics. If all of the processes and outcomes we associate with biological success can indeed be linked to the maintenance or increase of negative entropy, then this opens up the possibility of employing negative entropy as a common currency between apparently disparate aspects of fitness.

Whilst the theoretical reduction of fitness metrics to negative entropy is feasible, problems arise with the prospect of actually generating fitness measurements. Our current understanding of entropy – though still developing – does not allow for absolute measures of that quantity in the kinds of system in which a theory of natural selection is interested. Even if theory did allow for such measurements, the computations required would be intractable.

Despite the fact that we are barred from measuring fitness directly in terms of negative entropy, this thermodynamic approach still offers the considerable payoff of allowing for the conceptual unification of our previously disparate aspects of fitness, as well as the wider unification of our definition of life with our fitness concept. As a result, we can support the intuitively appealing statement that an organism with a greater biological fitness than another is "a more successful lifeform".

VI. Darwinian Populations

It would notionally be possible to conclude discussion at chapter five. However, I note that a good deal of my points in previous chapters would be severely undermined by a contradictory approach to defining the Darwinian population. This then necessitates discussion of the fourth assumption noted above – as to how we define Darwinian populations.

Several criteria have been put forward as definitive of the Darwinian population, with conventional approaches generally seeking to bind those individuals taken to be under selection together via some causal connection between them that is relevant to the outcome of that bout of selection. I follow Stegenga (2016) in conducting a systematic analysis of possible criteria by which to define the Darwinian population. Direct and indirect causal connections are examined, as well as other oft-cited criteria. However, I find that no single criterion is sufficient to delineate the Darwinian population in all cases. Indeed, I point to cases of parametric selection amongst asexual organisms as allowing for no such meaningful binding criterion at all.

Thus, I concur with Stegenga that a pluralist approach to defining Darwinian populations will be necessary in practice. However, I also explore one reason why the Darwinian population concept is so resistant to analysis and surrounded by apparently contradictory intuitions. Thus, I note that we also habitually assemble groupings to make comparative inferences as to causality within instances of selection. These "comparative populations" often overlap with the relevant Darwinian populations and are readily conflated, leading to confusion when we then attempt to find causal bonds between collections of entities where these might not exist at all.

4. Why Bother?

We can always ask what we hope to gain from any academic project. Why should we bother to challenge these assumptions? If they have been left undisturbed for so long, should that not indicate there is no benefit from destabilising them? Is this project to be conducted purely for rarefied academic interest, without any hope of wider implications, or do we expect there to be meaningful payoff in terms of progressing our understanding of natural selection more broadly?

Over the course of discussion, it will become apparent that the assumptions set out above have been serving to artificially constrain our understanding of natural selection across multiple fronts. Tackling each individual assumption will yield its own significant increase in the explanatory scope for our theory of natural selection, as erroneous limitations are removed. As well as extending our account of selection to new sets of scenarios, we will also gain the ability to better account for currently problematic instances, where theory seems to fail to correspond to our observations. For example, in chapter two, liberalising how we think about fitness allows us to regard the giant fungi of the *Armillaria* genus as biologically successful by virtue of the huge size to which they grow. The alternative, at present, is

simply leaving this clear biological success unaccounted for in selective terms because these fungi tend not to produce offspring as we might expect.

Now, it is worth noting that, across the various topics dealt with throughout this whole piece, there will be a general trend in my analysis in terms of moving away from the relatively simple, monist positions representative of conventional accounts of natural selection, and towards a more complex, pluralist view of that phenomenon. This is a trend that could be interpreted as a backwards step for theory. Traditionally, we associate theoretical advance, at least in part, with the parsimony of unifying, simple accounts. My fracturing and complexifying key elements in our understanding of selection could be seen as undesirable in this context.

Immediately, I would say that this increase in complexity must be balanced against the significant increase in explanatory scope it allows. However, despite my tendency towards pluralism across this piece, my analysis will also offer the promise of significant conceptual unification – if at a separate level of analysis.

As such, the "thermodynamic" approach to fitness I outline in chapter five is not capable of providing a working common currency measure to unite the different fitness metrics I identify in chapter two (persistence, somatic size and numerosity). Thus, at the practical level, fitness measurement would remain pluralist. However, my approach does unite these aspects of fitness at a conceptual level – explaining what they have in common, as well as what makes a metric valid and its specific use appropriate and meaningful. Simultaneously, my thermodynamic approach also allows us to unite our fitness concept with Schrödinger's thermodynamic definition of life within a single theoretical framework. In my final chapter, I also indicate that my "comparative population" idea might further synthesise with that framework. Clearly, all this would represent a significant increase in theoretical parsimony.

Overall, then, theoretical progress on a number of limited fronts as we challenge each individual assumption is accompanied by progress on a broader scale as we change how we think about the phenomenon of natural selection as a whole. I will return in the conclusion as to whether and to what extent my arguments across this piece add up to a net forward or backward step for our theory of natural selection. For now, though, we can at least see that there are potential explanatory and conceptual gains to be made.

I

STRUGGLE, COMPETITION AND SELECTION

There is a commonly held, but vague, idea that natural selection is a product of some kind of struggle or competition. Authors across both academic and popular works frequently discuss selection in this manner. However, they seldom, if ever, pause to give their assertions any explicit form. Indeed, authors often seem to write about selection in a fashion that actually runs counter to the content of their more formal statements as to what they take to constitute natural selection. In this first chapter, then, I will explore what role struggle and competition really play in selection.

I will explain that specifically zero-sum competition can indeed be a powerful driver of selection and that, where zero-sum contests are in force, they confer several "special" properties on instances of selection. However, I also defend the idea that selection can be driven by other forms of interaction between participants. Specifically, I will discuss cases of selection driven by mutualistic and exploitative interactions. Beyond this, I will also hold that selection can occur in cases without meaningful causal interaction between participants *at all*. In such cases, selection is instead driven by interaction with the general, abiotic environment.

Contra Godfrey-Smith, I hold that competitive selection is not necessarily any more powerful than the other forms of selection I identify. I show that many of the characteristic phenomena associated with competitive selection are also manifested within, or have close analogues emerging from, mutualistic and exploitative scenarios. Accordingly, I cast doubt on Godfrey-Smith attempt to establish a unique role for competitive selection in explaining the origin of novel adaptive traits. However, I show how selection of all forms can have a positive role in bringing forward new adaptive variants. I also note that, where selection is driven by mutualistic or exploitative interactions, it can be *more* readily applied to make Godfrey-Smith's "origin explanations" than where competition is the driver. Finally, I structure my findings into a new taxonomy of selection, intended to update that provided by Godfrey-Smith.

To make these points, I will structure this chapter as follows:

1. Struggle as Competition

I explain that the terms "struggle" and "competition" have tended to be used interchangeably in the literature around selection. Following this trend, I identify struggle simply with competition. I note the possibility of defining struggle without reference to competition but defer analysis of this idea until section seven.

2. Competition as Zero-Sum Competition

There are inherent difficulties in transposing the originally human notion of competition to the biological world. I defend my own identification of competition with zero-sum contest. However, I also note that – even if readers do not accept my identification of zero-sum contest with competition – this chapter can be read simply as an exploration of the role of such zero-sum interactions in selection, without tying that discussion to human ideas of struggle or competition.

3. Role in Contemporary Theory

I note a tension within many standard descriptions of natural selection, between narrative accounts of a competitive process and accompanying schematic specifications which themselves make no reference to competition.

4. Zero-Sum Interactions Are Special

I devote some time to exploring the particular qualities zero-sum competition can grant to instances of selection.

5. Is Zero-Sum Competition Unique?

Structuring discussion via application of the Lotka-Volterra equations, I show that selection can proceed via other forms of causal interaction between participants. I also show that selection is possible where interaction occurs only with the environment. Godfrey-Smith ascribes a unique capacity for competitive selection to be "creative" in accounting for the emergence of novel adaptive traits. However, I show his approach implies a highly dubious counterfactual. Via an argument adapted from Neander, I demonstrate that all the forms of selection I identify can potentially explain the origin of new traits. Indeed, I also show that mutualistic and exploitative interactions are more clearly creative in this manner than are competitive ones.

6. A New Taxonomy of Selection

My taxonomy of selection is intended to update the scheme provided by Godfrey-Smith. Borrowing terminology from game theory, I separate selection into "parametric" and "strategic" forms. I then subdivide strategic selection into competitive, mutualistic and exploitative types. Contra Godfrey-Smith, I accord no special significance to competitive selection and do not seek to impose any hierarchy between the forms of selection I set out.

7. Attempts to Partition Parametric Selection

Returning to issues from the beginning of the chapter, I discuss and reject Lennox and Wilson's non-competitive conception of struggle. This account would have the effect of partitioning my category of parametric selection, such that a subset of the parametric scenarios I identify would no longer count as selective. However, I show the distinction the pair attempt to draw is untenable.

Concluding, I note some of the downstream questions my points here raise for other elements of our wider understanding of selection. This leads into the issues addressed in subsequent chapters.

1. Struggle as Competition

The idea of some "struggle for existence" as part of the essential character of natural selection goes all the way back to Darwin, though there has been considerable debate as to what he meant by that phrase (Glymour 1999, Lennox and Wilson 1994, Lewens 2010, Ruse 1971). I will not be concerned here with any historical speculations as to Darwin's views. Indeed, it seems entirely possible that Darwin might not have had a fully consistent, worked-out conception for us to uncover. Even if he did, it would not have any necessary bearing on the scientific truth of the matter.

Whatever the historical facts, we find a confused situation at the current time. Natural selection is often described as involving struggle but, perhaps more frequently, selection is thought of as driven by some kind of competition. In any case, there seems to be little or no conscious differentiation between these terms, such that struggle is often considered simply in terms of competition. Distinctions between the two tend to be made only in the very scant philosophical literature on the matter - and with no great frequency, even there.

1.1. Struggle Without Competition

In this chapter, I follow common practice and identify struggle with competition. It should be noted, though, that this is not the only way one might think about struggle. After all, in normal language, we can straightforwardly describe struggle in the absence of competition. Thus, I would certainly struggle to run 26 miles, regardless of whether I was racing competitors in a marathon or simply trying to complete the distance on my own.

A few authors attempt to impose a non-competitive idea of struggle. They seek to capture the intuitive notion that an organism subject to harsh conditions might struggle, whilst one enjoying benign conditions might not. Lennox and Wilson (1994) develop a detailed account in this vein, attempting to define struggle with regard to population checks. However, I do not believe that any such account can be made to function. I will return to Lennox and Wilson in section seven, where I will briefly discuss why theirs and similar accounts of non-competitive struggle fail.

2. Competition as Zero-Sum Competition

In this chapter, then, I will identify struggle with competition and competition specifically with zero-sum competition. Thus, I will characterise what I mean by zero-sum competition, before providing some defence as to why I have chosen to define competition in this fashion.

In zero-sum contests, the success of one individual must inherently come at the expense of one or more of its peers. In the natural world, this will typically be manifested in competition for some limited resource – we might see individuals compete over food or mates, for example, where there is insufficient supply to satisfy all individuals' demands. Zero-sum conditions imply that, for one individual to have more food or to have mated more often, another must make do with less.

Zero-sum competitive interactions can be direct or indirect. For example, two animals might actively fight over resources such as food or mates, but might just as well starve or fail to reproduce simply because the relevant resources have already been located and sequestered by another individual. What is really characteristic across these cases is that outcomes for any individual are determined by how their traits *compare* to those of their peers, rather than to any *absolute* standard. This is a crucial distinction, which is perhaps best illustrated by an example. Let us imagine that we observe a herd of zebras chased by a pack of lions. If there are only a few – let us say three – lions and a large number of zebras, a zebra will only need to run faster than the slowest three of its peers to escape predation (assuming that once each lion has caught a zebra they will be busy eating it). We can think of the zebras

as involved in a zero-sum contest to escape predation, as not all of them can be successful (assuming that the lions are faster runners than at least a significant number of zebras) and success is based upon how one's performance or traits compare to that of one's peers, rather than to any absolute standard.

In this example, then, we perceive the nature of zero-sum contests, in that individuals will enjoy success at the expense of others. The zebras that survive do so at the expense of those that are eaten and they do so by virtue of the fact that they are *comparatively* faster than those that are caught by the lions. Had all the zebras been 5mph slower, the same three would have been caught and killed. However, if we changed the rank ordering of the zebras' speeds, things would be entirely different. Let us say that we made the current slowest three zebras the fastest. Now they would not be eaten but would be leading the charge away from the lions.

To clarify further, let us contrast a situation without zero-sum conditions. If we change the scenario so that there are more lions than zebras, the zero-sum element disappears. For a zebra to survive, it must now be able to run faster than any of the lions. How fast it is compared to the other zebras is irrelevant – the standard for success is now an absolute rather than relative one. If the lions run at 30mph in all cases, in the zero-sum context, a zebra could run at 20mph and still escape as long as three of its peers were even slower. In the second case, any zebra that wants to survive must be able to run at more than 30mph, regardless of how fast or slow the others are.

2.1. Why Zero-Sum?

Here, I will identify competition specifically with zero-sum competition. Many readers will automatically associate competition and zero-sum circumstances without any prompt, such that a justification of this position might seem redundant. However, it must be noted that “competition” is originally a concept describing human relations, which we artificially transpose to the natural world. Accordingly, any mapping will be imperfect, with room for debate as to how this idea should best be defined in the biological realm.

In selection, the main alternative to associating zero-sum contest with competition is to identify that concept simply with differential performance. This goes well beyond Darwin’s own remarks on competition, as well as how readers will think about biological competition in a contemporary context. However, there are indeed authors who attempt to apply such ideas of competition to selection. A typical remark is found in Glymour (1999). Having already identified struggle with competition, he states:

> "Competition" here is to be broadly understood to include not only competition for one or more limiting resources, but also differing susceptibilities to predation, climate, and disease, differing ecological dependencies, and so on. (Glymour 1999:186)

What precisely is meant to be entailed by such notions of competition is never fully explained by those who invoke them. However, it seems that this approach will be obliged to perceive competition in *any* case where there are differences in performance – certainly, there will not need to be any scarcity of resources. Competition thus becomes something we identify after the fact as observers, rather than a phenomenon with meaningful causal bearing on the events we observe. As such, where we see two variants reproducing at maximal rate with unlimited space and resources (as with Lewontin's Bacteria, introduced in section 5.5), we will apparently be obliged to regard them in competition so long as one is reproducing more quickly than the other – even though there is no scarcity and the two strains generally have no effect whatsoever on one another's behaviour. Certainly, there is no sense in which one such competitor "wins" at the *expense* of the other.

I would argue that competition so-defined becomes so utterly ubiquitous as to be without meaning. It would, in fact, become difficult to find individuals *not* to be regarded as in competition. Where a concept of competition is near-universal and carries no causal import, it seems totally uninformative and simply not worth our while in applying.

By contrast, zero-sum competition is not simply relative to an observer's perception, but makes a meaningful causal impact where it acts. Zero-sum competition will typically affect the behaviour of organisms involved, as well as their ability to survive and reproduce. Thus, organisms will inherently succeed at the expense of their peers, with relative performance dictating their share of some resource and ultimately becoming explanatory of their subsequent biological success. I will discuss the effects of zero-sum competition in more detail in section four. However, where our two differentially reproducing variants above are taken from their situation of boundless plenty and forced into zero-sum contest over scarce resources – say nutrients – there will likely be changes in their immediate behaviours, as well as their subsequent chances of survival and reproduction. Energy will typically be expended simply in the business of competition. Less competitively able individuals will have to make do with reduced nutrient supply and might produce fewer offspring if they do not starve to death first. Indeed, the stronger competitor might well drive the weaker to extinction. Over the longer term, zero-sum competition might even lead to adaptive arms races (again, explored in more detail in section four).

In short, then, zero-sum competition is causally efficacious where it comes into force. As we will note in section five, it is also not difficult to identify biological scenarios where zero-sum competition is not

in force. Thus, where we *do* note a system exhibiting zero-sum competition, to describe it as such is genuinely informative.

As a secondary point, I would also hold that zero-sum competition is the more convincing mirror in the natural world to the salient elements of human competition. Thus, if we see two runners making their way around a track, it would be strange to say they were competing simply because one crossed the finish line before the other. The athletes might just as well be having a friendly chat as they put in a couple of laps to warm up, or they might be holding constant pace as part of training. When our runners are truly in competition, this will have a meaningful causal impact on events. Friendly chat and keeping pace will disappear. Speed and overall energy expenditure will almost certainly increase as they vie to cross the line first. Most importantly, there will be a winner and they will be such at the expense of the loser. In a competition, crossing the line first will be associated with depriving the loser of some prize, whether that be simple bragging rights or a trophy at a tournament.

This said, the subjective element in deciding how best to transpose human concepts to the biological world ultimately makes for an analytic blind alley. Going forward, then, I will use the term "competition" to refer to zero-sum competition. Even if the reader is determined to retain a strong commitment to the idea of biological competition in terms of differential performance, they can still read this chapter simply as a specific analysis of the relationship between zero-sum contests and natural selection. In this mould, the actual content should still be interesting.

3. Role in Contemporary Theory

The typical description of natural selection as competitive appears to be at odds with more formal theories simultaneously espoused in the same places. Across academic and popular sources, natural selection is often described in narrative terms as resulting from differential success in competition, only to be followed with a more formal definition of selection omitting any requirement for such competition.

In Ridley's textbook "Evolution" (also quoted in my introduction) we find the following perfect example:

> The excess fecundity and consequent competition to survive in every species provide the preconditions for the process Darwin called natural selection. Natural selection is easiest to understand, in the abstract, as a logical argument, leading from premises to conclusion. The argument, in its most general form, requires four conditions:

1. Reproduction[...]
2. Heredity[...]
3. Variation in individual characters among the members of the population[...]
4. Variation in the fitness of organisms according to the state they have for a heritable character[...] (Ridley 1996:71)

Thus, a narrative account of selection based on competition is followed by a schematic statement of a version of the standard heritable variation of fitness conditions associated with Lewontin (1970), which contain no requirement for competition. Indeed, Lewontin himself explicitly notes (1970:1) that his criteria do not require any competition in terms of scarcity of resources; allowing that simple differential reproductive output by two types should be considered as an instance of selection, even where all resources are in surplus and there is no competitive or any other salient causal interaction between those types (we will return to consider this idea in some detail later – notably here in sections 5.5 and 5.9 and then also in chapter six).

One might charitably imagine that the narrative components of accounts such as Ridley's in fact function to convey some additional restrictions on the class of legitimate cases of selection. It might be, then, that we are intended to study cases of heritable variation of fitness as selective, only where they occur in a competitive or similar context. However, examining actual biological practice, this does not seem to be the case at all. In later sections, we will look at examples where working biologists study instances of selection clearly lacking any competition between participants at all.

4. Zero-Sum Interactions Are Special

Many "paradigm" (to borrow a term from Godfrey-Smith 2009) cases of selection are plainly driven by zero-sum competitions. For example, the entire category of sexual selection is concerned with the competition between members of one sex to secure matings with those of the other at the expense of competitors. Some (notably Van Valen 1973, 1975, 1976, 1989 – discussed in chapter four) have explicitly argued that we ought to regard zero-sum competition as a necessary component of selection.

Godfrey-Smith is one of the few authors to have dealt with the role of competition in selection in an explicit, systematic manner. He expects that full-blooded, "paradigm" instances of selection will be competitive and attributes important qualities to competition. Competition is one of the causal relations – along with factors including sexual reproduction and shared environments – which he cites as providing the "glue" to bind together "Darwinian populations". That is to say that Godfrey-Smith uses

these different relations as means to define the set of individuals involved in the same instance of selection. This idea will come to the fore in chapter six, in my analysis of the Darwinian population concept.

More importantly here, Godfrey-Smith also claims that only paradigm cases of selection allow us to make “origin explanations” (defined and discussed in section five) and that they do so by virtue of the presence of zero-sum competition. I will challenge this idea in section five. However, I certainly agree with Godfrey-Smith that instances of selection driven by competition have several highly significant features as a direct result of the competitive interactions between individuals.

I will now set out a few of these important features of zero-sum competitive selection in systematic fashion, so as to facilitate discussion in both the current and subsequent chapters. This will provide us with a much more precise understanding of what zero-sum competition “adds” to selection; which will, in turn, allow us to understand the limitations of competitive selection, as well as when non-competitive forms of selection might yield equivalent effects.

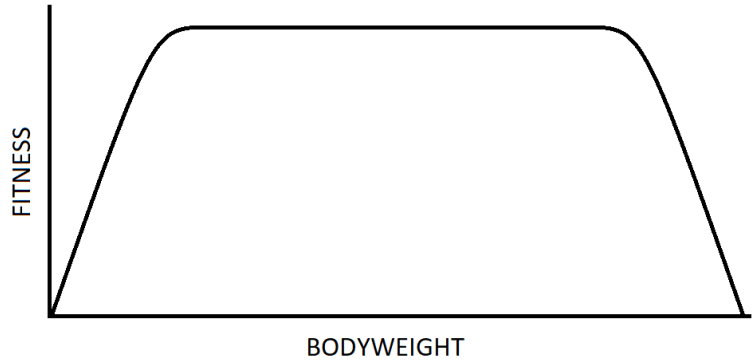
4.1. Adaptation That Continues Beyond Viability

As described above, an inherent property of zero-sum contests is that the success of an individual depends upon how it compares to its competitors, rather than to some absolute benchmark reflective of the requirements of the general environment. In practice, when selection is iterated over longer periods of time and the possibility of novel mutation is included, lineages will adapt to the selective pressures imposed by their competitors. However, this will in turn create new selective pressures for those competitors, who can then be expected to adapt themselves – leading in turn to new selective pressures and the need for fresh adaptation on the part of the first lineage, such that a cycle emerges.

This process of adaptation and counter-adaptation is often characterised as an evolutionary "arms race". These arms races are particularly interesting because they drive selection on lineages well "beyond" what is required for viability in their general, abiotic environment. Indeed, competition as I have defined it potentially allows selection and adaptation to continue indefinitely. As we will see, this is in marked contrast to what we would expect of selection proceeding without competition.

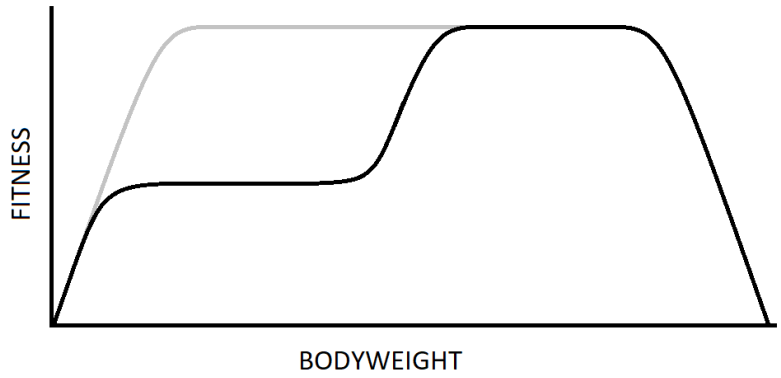
To be clear, when I say that competition drives selection "beyond viability", I do not mean that it necessarily delivers more or better variants than a non-competitive case (more on this idea in section 5.2). Rather, I mean that selection will have proceeded in winnowing the range of existing variants more extensively than the general environment will do by itself. A simplified example with a graphical representation will help clarify my point here. Let us imagine we have some species of animal where

isolated individuals are able to survive in their general, "abiotic" environments at a wide range of bodyweights. In graphical terms, we can show this "baseline" relationship in the simple plot of trait value versus fitness, below. In effect, this is an extremely low-dimension adaptive landscape.



Note the plateau region of the graph. Bodyweights here are equivalent in selective terms, as all are equally well suited to the environment. The more "extreme" bodyweights above and below the plateau region are selected against, as they inhibit the animals' ability to function in the environment. Being very large or small might cause problems for thermoregulation or movement, for example.

However, let us say our animals must compete in physical combat to secure matings. Larger individuals are more likely to win fights, and mates are limited, so smaller variants that are perfectly well adapted to the general environment are now selected against. This transforms our graph, or simple fitness landscape, into that below:



As noted, there is no increase in the variation available to selection. Competition has not caused any new adaptations to come into existence here. Instead, it has simply acted to narrow the range of viable types to a subset of those able to survive in the general, abiotic environment.

Even without its necessarily bringing forward new variants, there might be a temptation to think of competitive selection as narrowing down populations to the "best" variants in some *absolute* sense. Where competition selects for traits like physical size, strength or cognitive capacity, it seems to select individuals likely to prosper in a wide range of circumstances, such that we might see them as generally superior in some sense. In many scenarios, this will indeed be the case, and evolution guided by competitive selection will promote adaptations allowing individuals to better thrive in their general environments or even a broad range of environments. Humans, for example, might have developed their intelligence to better hunt prey species or to cheat their peers out of mates or food, but that same intelligence now allows them to use technology to expand their population by colonising many different geographies and to dramatically increase their life expectancy via medical science.

However, this generalised adaptation is far from a necessary feature of competitive selection. Often, competition will select for traits that are neutral or even negatively adaptive in the context of the general environment. Another example will help here. Suppose the males of some species come with either attached or detached ear lobes, with neither type enjoying any clear advantage over the other. Individuals with either trait occupy different positions within the same region of phenotype space, corresponding to viable male forms. However, if the females started to exert a strong mating preference towards males with attached ear lobes, such that those males did better in the competition for mates, then we can imagine that detached-ear-lobe-bearing males might eventually be eliminated from the population. Thus, we would see a trait that is perfectly viable in the general environment eliminated in favour of an apparently equivalent trait by the additional demands of competitive selection.

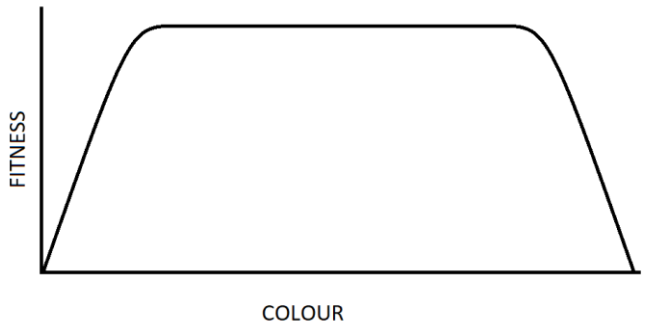
As noted, competition can even favour traits that are *less* well adapted to the general environment. Indeed, in many cases of sexual selection, this process has confined populations to regions of phenotype space that are *significantly* sub-optimal with regard to the prevailing environment. The standard examples here are the unwieldy tails of the peacock or the long-tailed widowbird (Andersson 1982, Krebs and Davies 1993:190-191). In either case, males equipped with more modest tails would more readily thrive in their general environment, but need to maintain their enormous plumage in order to compete for mates.

In sexual selection, we might also appreciate the power of adaptation driven by zero-sum competition to make selective change perpetual by virtue of selecting for arbitrary characteristics. As we have seen,

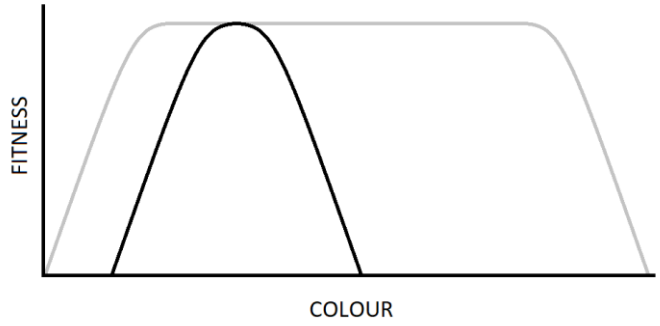
sexual selection can reward traits that are irrelevant or even somewhat damaging to an organism's survival chances in the prevailing general environment. If we add to this the possibility that the preferences of the "choosy" sex can change over time, then we might expect an unending string or cycle of different characteristics to be selected for. Sinervo and Lively (1996) note a similar effect where different male morphs in the side-blotched lizard constantly cycle through dominance in the population. We can think of the arbitrary traits favoured by sexual selection as akin to "signals". In principle, an infinite number of different specific signals can convey the same content, so long as the relevant code has been coordinated between the sender and receiver.

The result is a constantly transforming adaptive landscape, with a peak undergoing a random walk around a region of phenotype space corresponding to the range of trait values that are viable in the abiotic environment. Selection would potentially continue forever, though the individuals might never be any better suited to life in their geographic locale than they were to begin with. To make this abstract language more concrete, let us imagine that the male plumage of some bird species can take a range of colours, all of which are equally well adapted to the general environment. At any one time, most females prefer one colour above the rest, but this preference changes over time. The resulting graphs of fitness as a function of trait value at different times t_1 to t_3 are shown below:

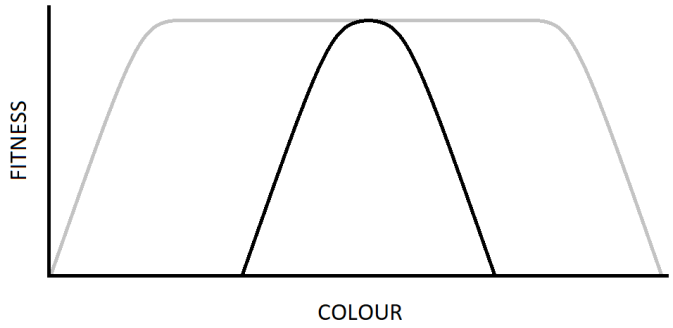
Adaptation to general environment:



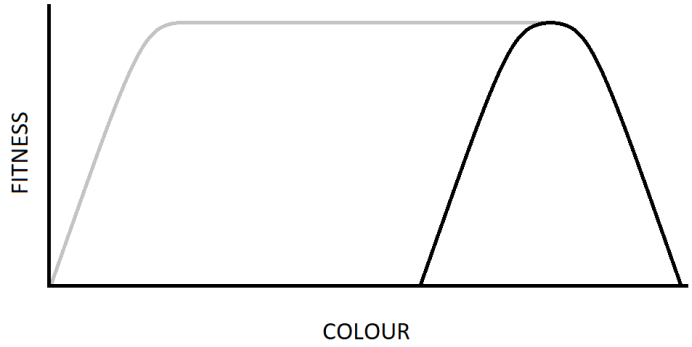
Competitive, t_1:



Competitive, t_2:



Competitive, t_3:



4.2 Competitive Exclusion

Zero-sum conditions inherently bring the possibility of competitive exclusion. This is the phenomenon that occurs when zero-sum competitions are allowed to run for a sufficiently long period of time, such that a more successful competitor drives its peers to extinction. Indeed, it was his observation of regular extinction rates within groups of organisms over time that prompted Van Valen (1973) to develop his novel, competition-based account of selection. Van Valen noted that what he saw was best explained by a constant emergence of new varieties leading to competition for the finite resources available within a niche. This in turn led to the competitive exclusion – that is, extinction – of some of the participants.

Competitive exclusion is an idea which accords with a typical, intuitive impression of selection, where the less well-adapted are eliminated over time (as in Ruse 1971). However, beyond intuition, competitive exclusion is an important driver of selection and evolution. This is especially true for the phenomenon of adaptive radiation.

4.3 Adaptive Radiation

Competitive exclusion helps us account for the propensity of selection to generate adaptive radiation. For Darwin, this was an especially important element of his theory (Lewens 2010) and in the *Origin* he

characterised, in particularly compelling metaphorical terms, something like what we would now describe as adaptive radiation:

> The face of Nature may be compared to a yielding surface, with ten thousand sharp wedges packed close together and driven inwards by incessant blows, sometimes one wedge being struck, and then another with greater force. (Darwin 1859:67)

In zero-sum circumstances, the only immediate way to actively escape being driven to extinction at the hands of a superior competitor in some resource competition is to de-conflict by switching one's reliance to a different set of resources. This might be the same resource-type in a different location or some other resource-type in the same location. Thus, if one encounters strong competition when hunting rabbits, one might continue to eat rabbits, but go looking for them in a different area, or one might stay put and get used to fishing instead. In different language, we might say that organisms can move to a new ecological niche to avoid extinction in their current one. This selective pressure to differentiate so as to avoid the risks of competition allows us to explain at least some cases of speciation with a mechanism driven by selection itself (Doebeli and Dieckmann 2000) in a manner highly reminiscent of Darwin's own remarks.

Ready examples of this behaviour might be found in the adaptive radiations of the Galapagos finches (Tebbich, Sterelny and Teschke 2010) and Lake Victoria cichlids (Turner 2007). It is easy to see that if all the finches on an island were in fierce competition for a limited amount of some foodstuff, then adaptations allowing one group of finches to live off another foodstuff will mean that they escape competition. With the Galapagos finches, we do indeed observe that adaptive radiation has allowed for a set of closely related species to occupy the same geographic region simultaneously, without competing with one another for food – notably, by the emergence of different shapes and sizes of beak, allowing exploitation of different foodstuffs.

This selective drive to evade extinction by finding new niches might at least partially explain the familiar trajectory of life's evolution to explore all possible geographical regions and all possible resources within any specific region. Thus, we see a full spectrum of species taking up each trophic level from detritivore to apex predator, right across the different regions of the world – that is, to exploit all possible niches.

5. Is Zero-Sum Competition Unique?

We have seen that zero-sum competition contributes a number of powerful qualities to selection. However, in itself, this does not rule out the possibility that other kinds of interaction between those under selection might make a similar contribution. With a few equations to help structure discussion, I will investigate different kinds of causal relationship which might hold between members of a Darwinian population. I will find that cooperation and exploitation relations can yield very similar – perhaps even more powerful – results to competition.

5.1. Formalising Matters

A neat way to model the effects of zero-sum competition on a population is with the Lotka-Volterra equations. These are derived from the logistic equation, shown below, which is commonly used to model "unfettered" population growth.

$$\frac{d\mathrm{N}}{dt} = \mathrm{rN}\left(1 - \frac{\mathrm{N}}{\mathrm{K}}\right)$$

Where:

N is the population size

r is the intrinsic growth rate

K is the carrying capacity of the environment

However, the Lotka-Volterra equations add terms accounting for the magnitude of competitive interactions between two variant populations. The resulting formulae are a good abstract representation of resource competition[1]. In a biological context, they are most often used to model competition between members of different species. Thus, (as per section 5.7) a typical use for the Lotka-Volterra equations is in modelling predator-prey cycles. Here, though, I follow Godfrey-Smith (2009:52) in applying this kind of model to capture the same dynamics where they hold between conspecifics[2].

Some formalisation will be useful in exploring the phenomena resulting from interactions amongst individuals under selection together. This step will also significantly facilitate discussion of Godfrey-Smith's position on the explanatory capacity of competitive selection. I must make clear, though, that it is not my intention to be rigidly bound by the Lotka-Volterra equations. Rather, they simply provide a

[1] Indeed, the Lotka-Volterra equations are also used in economics to model the competition between firms – as per Marasco, Picucci and Romano (2016).

[2] In chapter six, I will pick up on points made in this chapter to argue that Darwinian populations need not be limited to members of a single species – retrospectively rendering this distinction between uses of the Lotka-Volterra equation less salient.

convenient vehicle to explore the different characters of causal relationship that can hold between members of a Darwinian population. My analysis does not rely on the specifics of this particular model, and the same points could be made with any set of equations capturing the same physical phenomena. Instead, setting in place some more formal foundations will make it easier to generalise the kinds of behaviours we will examine so that we can more readily appreciate the action of similar causal mechanisms in apparently disparate real-world scenarios. As it happens, Godfrey-Smith also makes reference to the "alpha" values associated with the Lotka-Volterra equations in his discussion of competition (2009:51-52). Thus, making use of those equations also allows me to directly address his account.

For two competing types, then, the Lotka-Volterra equations come as a pair, expressing the rate of change of the number of one type as a response to the momentary number of the other. These equations are shown below:

$$\frac{d\mathrm{N}_x}{dt} = \mathrm{r}_x \mathrm{N}_x \left(1 - \frac{\mathrm{N}_x}{\mathrm{K}_x} - \frac{\alpha_{xy}\mathrm{N}_y}{\mathrm{K}_x}\right)$$

$$\frac{d\mathrm{N}_y}{dt} = \mathrm{r}_y \mathrm{N}_y \left(1 - \frac{\mathrm{N}_y}{\mathrm{K}_y} - \frac{\alpha_{yx}\mathrm{N}_x}{\mathrm{K}_y}\right)$$

Where:

N_x is the number of type x

r_x is the intrinsic growth rate of type *x*

K_x is the carrying capacity of the environment for type *x*

α_{xy} is the degree of effect of type y on type x

5.2 Alpha Values Greater than Zero - Competition

For zero-sum competition to hold in general, the success of one entity must inherently come at the expense of some set of peers. Within the Lotka-Volterra equations, this fact is accounted for by the alpha values. These coefficients quantify the extent to which one group influences the other – specifically the extent to which each new individual of one type causes the diminution of the other population. The examples of competitive selection we have seen so far correspond to cases where the alpha values will be positive. In the Lotka-Volterra equations, alpha values are coefficients to a term that is subtracted from the unbounded growth modelled in the parent logistic equation. As such, positive alpha values will encode that the growth of one group causes the diminution of the other – precisely the success of one at the inherent expense of another characteristic of zero-sum selection. For example, in

a competition over food, if $\alpha_{xy} = 1$, then each individual of variant *y* sequesters food such that their presence means that one fewer *x* can be sustained. We can imagine that each new *y* might be directly stealing food from *x*'s, though this need not be the case in practice. Godfrey-Smith (2009:52) states that, in his paradigm cases of selection, he would expect alpha values to be around +1, meaning that each additional member of one group causes the removal of one individual from the other.

5.3. Godfrey-Smith on Competition and Explaining Novel Adaptation

The most important – and apparently unique – quality Godfrey-Smith ascribes to competition is to allow for selection to be invoked in the explanation of how new adaptive traits come into existence – that is, in making what Godfrey-Smith calls "origin" explanations.

Godfrey-Smith differentiates two kinds of explanation we might make in an evolutionary context. These are "distribution" and "origin" explanations. Thus, of the former, Godfrey-Smith (2009:38) says "when we give a distribution explanation we *assume* the existence of a set of variants in a population, and explain why they have the distribution they do, or why their distribution has changed". As an example, if we noted a significant uptick in the number of people with red hair over a number of generations, we might offer a distribution explanation for why the number of redheads is increasing – perhaps referring to sexual selection by individuals preferring red-headed mates.

By contrast, Godfrey-Smith (2009:38) describes origin explanations as "directed on the fact that a population has come to contain individuals of a particular kind *at all*. It does not matter how many there are; the point is just to tell us how there came to be some rather than none." Thus, we might provide an origin explanation for the emergence of the trait of having red hair, where previously a population contained only blondes and brunettes. This would likely refer to the mutation of a relevant allele in generating the red-haired phenotype.

These forms of explanation map onto two senses of the word "adaptation". Thus, we would describe a population as undergoing adaptation when the frequency of types changes in response to selection. In this sense, we might say that a population had adapted when it was exposed to a toxic chemical which killed off all those unable to tolerate it. This change in frequencies of existing variants would be subject to a distribution explanation. However, we also use the word adaptation to refer to the emergence of novel traits which allow individuals to deal with selective pressures better than their predecessors. Thus, when we see Galapagos finches develop a new beak shape better suited to exploiting a new food source, we might also say that this was an example of adaptation. An explanation of how that beak shape came into existence in the first instance would be an origin explanation.

There is an extensive literature on whether we can regard natural selection as a creative force, understood in terms of our ability to refer to selection as part of our explanation of novel adaptation – that is, to make Godfrey-Smith's origin explanations. Thus, if selection can help bring forward new traits, this will mean it can be cited in explaining those traits' emergence. This debate is associated most strongly with an exchange between Sober and Neander (Neander 1988, 1995a, 1995b, Sober 1980, 1984, 1995, reviewed in Walsh 1998). To the layperson, it might seem perverse that we cannot explain the adaptations we perceive in the natural world as products of natural selection. However, the back-and-forth between Neander and Sober shows that it is actually far from straightforward that selection explains adaptation, with work required to show that selection can be more than a "winnowing" process.

Godfrey-Smith's own approach to demonstrating that natural selection can indeed be positively creative starts from the idea of cumulative selection. Thus, Godfrey-Smith notes that the complex adaptations we observe in real organisms will generally not emerge from single instances of mutation, but will rely on a certain sequence of mutations accumulating over evolutionary time, each building upon its predecessors. His example is the evolution of an eye, which does not suddenly emerge as the result of one single mutation, but as the endpoint in a cumulative, step-wise progression, with each stage presumably offering an adaptive advantage over the last.

Taking Godfrey-Smith's (2009:39-42) own example then, suppose that the trait of having a fully formed eye had an immediate precursor "X" – a slightly less effective system for visual sensation. One mutation will make the step from X to a full eye. Now, the chance of this mutation taking place within a given period of time will depend on the number of existing instances of X. More Xs will mean more chances to mutate into a complete eye. Thus, any mechanism which can increase the absolute number of Xs will increase the probability of a complete eye emerging within a given time. In turn, then, this means that a mechanism that can increase the absolute numbers of Xs will be relevant in providing an origin explanation of how a fully formed eye came to be.

Godfrey-Smith argues competitive selection will fulfil this role. Thus, say that X had its own precursor W – a slightly less effective visual system again, which X came to replace. Godfrey-Smith claims that, from the initial emergence of the first, solitary instance of X, through its spreading in the population and eventually reaching fixation, competition increases X's absolute number.

Ostensibly, this might seem plausible enough. However, note Godfrey-Smith is claiming (and his argument requires) that competition increases the *absolute number* of X and not its *frequency* in the population relative to W. Indeed, Godfrey-Smith explicitly acknowledges this distinction and is insistent that competition allows absolute numbers to be raised. However, it is far from obvious that

competition has the capacity to increase absolute numbers in this fashion. If this were the case, it clearly implies the counterfactual that, had competition not been in force, then the absolute numbers of X would have been lower – that is, had there not been some competition over scarce resources or similar between X and W, fewer X's would be in existence.

To assess this counterfactual, we need to know what the notional "baseline" population would be in the absence of competition. We can then determine whether competition has increased the numbers of any variant over and above that level. The problem, though, is that we lack any clear idea of what that non-competitive population would have looked like.

For example, suppose we observe a species where males compete for mates. In this species, some successful males will secure multiple females and some unsuccessful males will fail to mate at all. What is the relevant comparison here? When we think of what it would be for one male to have no competition, is that a situation where he has as many matings as he can manage? This would make some sense, as it would be equivalent to being a very successful competitor in the situation we observe, and – in very human terms – having no competition arguably means winning by default. Also, competition arises from a shortage of some resource – mates in this case – so it seems reasonable that the removal of competition ought to correspond to the relief of any such scarcity.

Certainly, that is one way of thinking about the matter. Alternatively, though, there is a case to be made that the correct counterfactual might be that males are simply paired with females one-to-one. The rationale would be that competition leads to an uneven distribution of mates, so the non-competitive alternative would be an even division. This solution has the apparent merit in that it does not require us – if we retain all the males from the competitive case – to imagine conjuring up a limitless supply of females, as we would in the hypothetical above (an alternative would be to remove sufficient males to eliminate competition, though then we might wonder where they all disappear to). However, this approach brings with it the, perhaps odd, result that the more successful males in the competitive scenario will apparently acquire fewer matings in the non-competitive scenario, as their inferior competitors are removed. It seems strange for an already-winning competitor to do worse when the opposition fails to show up.

One case might seem more or less intuitively obvious to different readers. However, both are very much hypotheticals. In reality, we observe only the competitive arrangement, and so any alternatives will generally be confined to our imaginations (relevant empirical comparisons might be available in some cases, but this will not be universal). In our example here, both cases are empirically implausible in different ways, but we have no absolute way of saying which is a more appropriate comparison. In

evaluating counterfactuals, Lewis (1973) instructs us to prefer the option differing least from the real, observed world we seek to explain – though making this choice objectively is difficult in practice (Weatherson 2016:§3.3). In this case, both scenarios are clearly fantastical and far from our own world, leaving us with the seemingly intractable problem of which fantasy world is most like real life. Searching for an absolutely true answer looks to be a fool's errand and, in practice, answers are highly likely to be infected with personal intuition.

For Godfrey-Smith's account to work, he needs us to make use of counterfactuals more similar to the second approach above (that of an equal division of males) than the first. This is because he requires that some variants do indeed perform better in the presence of competition than without it – otherwise, competitive selection cannot be thought of as increasing the absolute numbers of those variants. My own intuition on the subject – as far as this matters – happens to be very different to Godfrey-Smith's. Thinking about the matter formally, we move from the logistic equation to the Lotka-Volterra equations, as noted, by *subtracting* a term to account for negative adjustment to a variant's population growth. When Godfrey-Smith states that he expects alpha values to be of the order of +1, he ensures that this term will still subtract from the "unfettered" variant population size. Thus, it strikes me as strange that he regards it as obvious that competition will cause an absolute increase in the numbers of a successful variant. He does not pause to clarify by comparison to a specific counterfactual or otherwise show why this is the case.

To be frank, whilst he does not give all that much detail on the quantitative side of things, it sounds rather like Godfrey-Smith imagines these terms to have the opposite of their actual mathematical effect within models. In the Lotka-Volterra equations, we can see that, to increase variant numbers beyond their levels in the logistic equation in this manner, the alpha values fed in would have to be negative. Actually, as we shall see in an upcoming section, negative alpha values do occur in nature (as Godfrey-Smith notes – 2009:52,56) and can be powerful drivers of cases of selection, which are clearly relevant to origin explanations. However, these negative alpha values do not correspond to instances of competition.

5.4. A Detailed Account From Nanay

Whilst Godfrey-Smith skips ahead without explanation, Nanay (2005, 2010) makes an analogous argument but provides much more detail on his reasoning. Like Godfrey-Smith, Nanay holds that cumulative selection can be relevant to the explanation of adaptation in the presence of resource competition where this leads to increases in the absolute numbers of adaptive variants. However, Nanay is aware that the argument hinges on a counterfactual and provides some insight into just which

counterfactual scenario he is using to reach his conclusions. Thus, we can use Nanay's more developed account as a stand-in where Godfrey-Smith does not explain his position.

Nanay begins with a case where resource scarcity caps a population, such that the survival of individuals of one type will necessarily mean the death of some of their peers. This is precisely the kind of zero-sum circumstance we have been dealing with. In Nanay's scenario, then, offspring from well-adapted lineages will tend to survive, with this meaning those from poorly adapted lineages will tend to lose out and perish. So far, so good. However, for Nanay to show that selection can be creative in the way he means to, he must show that the well-adapted here are enjoying greater success than had selection not operated at all. He does this by contrasting a non-selective counterfactual case where the population remains capped. In this case, it seems that the well-adapted lineages will have to bear a larger share of deaths, rather than these being disproportionately suffered by the maladapted. As such, the total number of deaths remains constant, so that the population size continues to track at a steady level. This is equivalent to the second kind of counterfactual discussed above, where mates are shared equally.

Nanay sets out this counterfactual in an attempt to deal with another possible issue stemming from this style of reasoning. Unfortunately, he does not defend his choice of this specific counterfactual or address the idea we have just discussed, that there might be more than one way to think about removing selection in competitive scenarios. As it is, though, the non-selective counterfactual Nanay puts forward rings rather hollow. The problem ultimately derives from the idea that it is possible to separate the intensity of selection from restriction on population growth. If resources really are scarce – such that this caps the total population and in turn necessitates that reproductive success by one lineage is contingent on deaths or failure to reproduce in others – then selection will be as a *direct result* of the capped population. The population cap and the scarcity leading to resource competition will thus, very literally, be the same thing. If this is not the case, then a constant population size would have to be maintained by a harsh abiotic environment or similar and it will not be true that there is actually a scarcity of resources, where this is a causally meaningful statement.

As a result, it makes very little sense to attempt to relax selection but maintain a population cap – the two are one and the same. Competitive selection is what maintains the population at a certain level and removing it would imply allowing for population growth. If we embrace that idea, though, we arrive again at the first kind of counterfactual discussed above; that is, in a position where competitive selection only acts to reduce the absolute reproductive output of those involved – even successful, well-adapted variants. As noted, this does not allow for competitive selection to be relevant to origin explanations.

Of course, both of these kinds of counterfactual contain practically impossible or implausible – essentially fantastical – elements which mean that neither can be objectively put forward as an unassailable favourite. This includes both the egalitarian distribution of causeless deaths accompanying Nanay's (and presumably Godfrey-Smith's) approach and the inexhaustibly bountiful supplies of mates or material resources in the non-selective scenarios I have outlined. Either way, there is scope for objection for those whose intuitions are unsatisfied. As before, I do not intend to argue that the counterfactual according with my intuitions is the better one. Rather, it simply seems wise to realise that any definitive conclusions on this matter are founded on sand [3].

5.5. Possible Origin Explanations Due to Competitive Selection

To Godfrey-Smith's credit, there is a more mundane manner in which at least a subset of cases of competitive selection can be relevant to origin explanations. Neander (1995a, 1995b) makes use of cases of selection featuring sexual reproduction and cumulative selection to argue against points made by Sober (1980, 1984, 1993, 1995) to the effect that natural selection cannot feature in origin explanations at all.

Neander's original examples are not ideal for our purposes here, as her own discussion retains a commitment to selection raising absolute numbers – which will ultimately imply a similarly dubious counterfactual to Godfrey-Smith's (indeed, Neander offers something of an appeal to intuition in defending her position in 1995a:77-78). However, we can devise a modified version of Neander's argument which still makes use of sexual reproduction and a form of cumulative selection to demonstrate a creative role for selection.

Thus, we can show that selection does not have to change the absolute numbers of any one variant to facilitate the emergence of new traits. Rather, it can simply change the relative frequencies of variants. This is because, in many cases, novel adaptations might come about by combination in the same individual of traits or genes already present in the population in separate individuals. For sexually reproducing species with anything short of fully assortative mating, changes in the frequencies of variants will affect the probability of individuals being produced with novel combinations of traits.

Let us consider selection at a single locus in a population of sexually reproducing organisms. Two alleles, A and B, correspond to our locus of interest. The vast bulk of the population are homozygous for B (BB) and a few individuals are heterozygous (AB). No individual has yet been born which is homozygous for A (AA). Heterozygotes enjoy a minor selective advantage over homozygotes for B,

[3] It should be noted here that Lewens (2015:11) reaches a similar conclusion as to Godfrey-Smith's position on competition and origin explanations but via a different and much briefer argument.

with homozygotes for A enjoying a major selective advantage over all types. Mating is effectively random and the rarity of the heterozygotes makes it very unlikely that two will mate and produce a homozygote for A.

However, suppose that, over time, the action of selection reduces the BB segment of the population, whilst leaving the heterozygote segment intact at its starting value. As the number of BBs decreases, the probability of two ABs breeding with one another increases, thus increasing the probability of an AA individual emerging. We can think of BBs getting in the way of ABs meeting one another. If and when two ABs do meet and produce an AA, we will thus be able to cite selection as a facilitating factor, making it part of the explanation of the origin of a new trait. Selection has effectively acted to remove the barriers between ABs.

The selection which leads to the change in frequencies of the BB and AB variants might be driven by competition, but it might just as well not be. All that is required is a change in the *relative* numbers of variants. In our example, the initial probability of two heterozygotes meeting to breed would be the same whether they were 10 in a population of 10,000 or 1000 in a population of 1,000,000, whilst the odds of two heterozygotes finding one another would be improved by the same degree if selection changed those populations to 10 in 1000 and 1000 in 100,000, respectively.

As we will see in subsequent sections, *any* form of selection can become relevant to origin explanations in this manner when combined with sexual reproduction[4]. Competitive selection might become especially relevant here, though, in allowing for a more rapid change in the relative frequencies of variants by actively eliminating the maladaptive. By acting as an accelerant in this process, selection driven by competition becomes explanatorily relevant to the emergence of new adaptations resulting from recombination due to sexual reproduction.

5.6. Alpha Values Less Than Zero - Mutualism

The specification that alpha values must be greater than zero for us to observe zero-sum competition raises the question of what the case might be if these coefficients took significantly different values – say, becoming less than zero. Is this logically possible, does it happen in practice and what are the implications for selection if so? In short, the answers here – entirely unsurprising to any student of ecology or economics – are "yes", "yes" and "often highly significant".

[4] Note that this argument could be expanded beyond sexual reproduction, to any case where there is recombination of genetic material between adjacent individuals. As such, horizontal gene transfer in the bacterial world should also allow for the relative frequencies of types to influence the origin of new traits. However, I will not explore this idea here.

A biological scenario of the kind modelled by negative alpha values would be a cooperative or "mutualistic" one, where two groups actually benefit from the presence of one another, allowing them to grow at a higher rate, and/or potentially sustain a larger population, than if one of them had occupied the same environment alone.

Godfrey-Smith (2009:63) makes very brief mention of mutualistic interactions resulting from negative alpha values; though he appears not to consider scenarios featuring them as selective – certainly not in the paradigm manner he reserves for competitive scenarios. However, we can see any number of cooperative interactions driving selection in dramatic ways, often generating analogous results to competition.

Many of the most striking and well-known examples of selection driven by this kind of interaction are of insect/plant mutualisms. In pollination, for example, both plants and insects develop various signals and anatomical features to facilitate the location and harvesting of nectar and collection of pollen from flowers. Insects evolve the sensory apparatus to efficiently seek out flowers and the feeding apparatus to siphon off nectar. In turn, the flowers evolve various structures that function in concert to guide the insect to the anthers and ensure it leaves with pollen as well as nectar. For the well-known "ant plants", trees develop hollow vessels where a colony of ants live and from where they, in turn, defend the tree against browsing herbivorous species (Rico-Gray and Oliveira 2007).

Such cooperative relationships can lead to more and more adaptations as the participants reciprocally respond to complement changes in one another's phenotypes over long periods of time. This steady accumulation of complementary adaptations might be thought of as the cooperative equivalent of a competitive arms race or Red Queen Effect. As such, we observe evidence of selection driven by cooperation, where this is qualitatively similar to selection driven by competition.

The specific direction of the resulting adaptations might share something more with such arms races, or the results of sexual selection, in having an arbitrary component. This might be observed in cases where the mere fact that traits are coordinated matters more than the specific character of the traits themselves. For example, when organisms evolve means of signalling one another, the particular signal employed could take many forms so long as it can be received and interpreted effectively. As such, a pheromone and the receptor detecting it could each evolve many different, complex functional configurations, and do so in a cumulative fashion, so long as they evolve in concert and thus interact effectively with one another. This would be akin to the arbitrary characteristics which can be latched onto by sexual selection.

One possible difference between adaptation driven by cooperation as opposed to competition is that the former might be expected to reach an optimum endpoint and cease, rather than continuing indefinitely as with competitive arms races. However, given that many mutualisms rely on quite literal signalling between participants, it seems that there might be some scope for endless, adaptively neutral random walks as to the precise form of that signal; analogous to the endless, arbitrary change made possible by sexual selection.

It is particularly interesting to note work suggesting that mutualism can lead to speciation via a similar mechanism to that caused by competition (Doebeli and Dieckmann 2000). We can certainly imagine an insect species differentiating to form mutualisms with multiple different plant species. This means that cooperation can also form part of explanations of adaptive radiation and thus underpin a characteristic part of Darwinian theory.

5.6.1. Negative Alpha Values and Origin Explanations

As we can see, competition is not the only kind of interaction between individuals which can drive selection. We know this in principle via formal treatment and also by observation throughout the biological world, where we can find an abundance of mutualistic relationships conferring adaptive advantages to their participants.

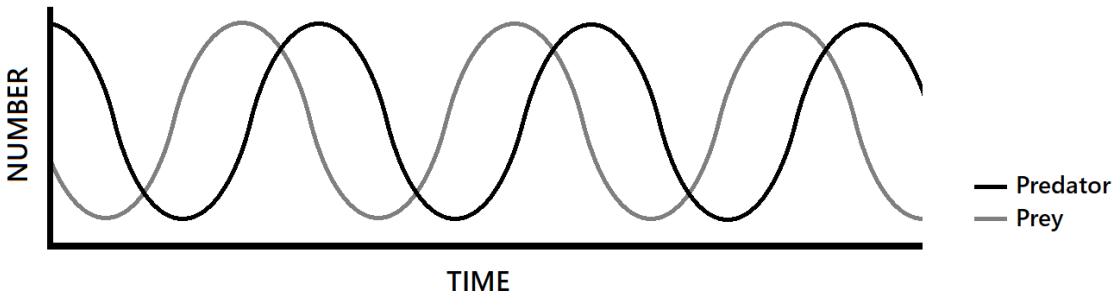
In fact, selection driven by cooperation seems to be more powerful than competitive selection in its ability to clearly increase the absolute numbers of the variants that benefit from it. When we introduce mutualism, we plainly inflate the numbers of participants, over and above whichever baseline one wants to consider. The same ambiguity around appropriate counterfactuals, discussed above, simply does not hold. Quantitatively, in the case of cooperative selection, when we move from the logistic to the Lotka-Volterra equations, negative alpha values mean we are adding a positive term to baseline population numbers. Empirically, we know that mutualisms must offer real advantages to participants over making do alone as, otherwise, those mutualisms would not evolve.

Regarding Godfrey-Smith and the issue of adaptation and origin explanations, selection driven by cooperation actually functions to bring about adaptation in a much more clear-cut way than does competitive selection. Indeed, cooperative selection functions more like Godfrey-Smith's description of competitive selection than competitive selection does itself. Since mutualism increases the absolute numbers of well-adapted individuals, we increase the probability of subsequent mutations which build upon the currently advantageous traits. As such, we can cite cooperative selection in explanations of how such new adaptations come about.

5.7. Mixed Alpha Values - Exploitation

Do both alpha values need to be positive or negative at the same time? Looking to nature, the answer is no. Lotka-Volterra equations with one positive alpha value and one negative are commonly used to model predator/prey and parasite/host interactions (as noted, the Lotka-Volterra equations are best known as a model of predator/prey interactions). For a predator, the larger the population of the prey species, the better, as there will be more food to be had. By contrast – and fairly obviously – for the prey species, the more predators to contend with, the more difficult life will be. These simple facts are expressed by mixed alpha values. The positive alpha value will express the action of one predator/parasite upon the prey/hosts and the negative value the effect of one prey/host upon the predators/parasites. I will refer to cases of selection driven by this kind of interaction as "exploitative".

When a predator species is heavily dependent upon a single prey species, we can observe the well-known predator-prey cycle as an example of an important dynamic governed by this kind of relationship (as per Gilpin 1973). When this cycle occurs, we see a repeating sequence of events, beginning with the predator population growing as it exploits a plentiful supply of prey. However, as the number of predator individuals increases, the numbers of prey are suppressed by increased predation. In turn, this causes the predator population to collapse as food becomes scarce, with the subsequent respite from predation allowing the prey population to quickly expand, returning to the beginning of the cycle. Graphically, this approximates a pair of offset sine waves and is shown below:



The exploitative interactions of the predator-prey cycle generate perpetual selective change in a different manner to the arms race or random walk-type processes we have seen so far. In an ideal case, this oscillating selection could indeed be expected to continue indefinitely. In practice, though, one might expect some equivalent to the "damping" of mechanical oscillation to cause the population swings to become less severe and a static equilibrium to emerge.

We also frequently observe adaptive arms races between predators and prey or parasites (including pathogens) and hosts, with these races being very similar in character to those between individuals

involved in competition. Examples are found everywhere in nature, from the reciprocal escalation of camouflage and sensory systems, to the back-and-forth evolution between toxins and their tolerance, to the development of immune systems and of pathogens' means to circumvent them. These kinds of arms races have the potential to continue indefinitely by cycling through arbitrarily different regions of phenotype space in much the same way as we have already observed in sexual selection and the signal-type coordination between partners in mutualism. A good example is the constant changes in surface antigens required for a flu virus to continuously adapt as its host immune system becomes accustomed to recognising, and thus combating, each new variant.

5.7.1. Mixed Alpha Values and Origin Explanations

With selection driven by exploitation interactions, we again see the kind of special features which we had originally associated only with competitive selection. Indeed, in chapter three, section 5.3, we will see that selection driven by both kinds of interaction can give rise to the same characteristic “boom and bust” population dynamics associated with the competitive fluctuating selection observed between, for instance, Sinervo and Lively’s (1996) side-blotched lizard morphs.

In terms of adaptation and the capacity for origin explanations, the presence of a least some negative alpha values means that exploitative selection offers the same kind of clear-cut means for explaining the emergence of new adaptations as did cooperative selection. Specifically, on the "predator" side of the interaction, exploitation will serve to boost absolute numbers of individuals, increasing the probability of subsequent adaptations and thus becoming part of how we explain those adaptations. As before, that exploitation raises the absolute numbers of the "predators" involved is much more obviously true than the idea that competition absolutely benefits successful competitors. When a carnivorous species starts predating a new herbivore species, the carnivores' absolute numbers will increase in line with this new addition to their available food resources. Just as before, we can be sure of this general point as exploitation relationships – predation, parasitism and the like – would simply not have evolved if they did not favour the relevant predator or parasite.

It is worth noting that the absolute increase in numbers gained by a variant in exploiting a new resource or niche also allows us to put the idea, mentioned previously, that natural selection can actively promote adaptive radiation, on a much firmer footing. If we think about adaptive radiation only in strictly competitive terms, then we encounter the same issue as regards counterfactuals and origin explanations which I have already discussed at some length. In short, it becomes difficult to claim with any certainty that selection actually hastens or is positively

> responsible for adaptive radiation. However, when we take account of the very real increase in absolute numbers to be gained via exploitation relations in entering new niches, we can cast natural selection in a more definitely creative role as a driver of adaptive radiation.

5.8. Alpha Values Equal to Zero

In a circumstance where both alpha values equal zero, the Lotka-Volterra equations collapse back to the standard logistic equation (since the second term in the bracket becomes equal to zero). In terms of real-world scenarios, this represents a situation where we observe the differential success of two types simply as a result of how well they interact with the environment, rather than because of any competitive, cooperative or exploitative interactions with one another.

The *tour de force* example here is Lewontin's (1970) oft-cited scenario (alluded to previously), whereby two strains of bacteria grow exponentially in the same vessel with an excess supply of nutrients so that they do not come into competition with one another. Lewontin states that:

> ...the element of competition between organisms for a resource in short supply is not integral to the argument. Natural selection occurs even when two bacterial strains are growing logarithmically in an excess of nutrient broth if they have different division times. (Lewontin 1970:1)

I will return to this scenario repeatedly throughout subsequent chapters and will refer to it simply as "Lewontin's Bacteria". What is important here, though, is that Lewontin insists this scenario is an instance of selection, simply by virtue of the differential growth rate of the two strains – despite the fact that they will have no meaningful causal interactions with one another. For Lewontin, since the requirements of the standard heritable variation of fitness criteria for selection – which he sets out on the same page – are met, we are observing selection in action, regardless of a lack of competition or similar.

Despite Lewontin's certainty, many have found this scenario unpalatable as a case of selection (Lennox and Wilson 1994), with the general idea that what is lacking is some kind of causal connection – most likely a competitive one. If we cast our mind back to the apparently contradictory narrative and schematic statements of selection I noted as common across academic and popular sources, Lewontin's Bacteria provides us with a case which accords with the schematic requirements (there is heritable variation in fitness) but not the narrative descriptions (there is no struggle for existence or scarcity of resources). The fact that the narrative descriptions are so vaguely constructed, though, means that those

encountering these "non-interactive" cases are left without much inkling of what it is they wish to say is missing.

The two responses which tend to be made are either to follow Lewontin, and wholeheartedly embrace the idea of selection with no causal interactions between the participants, or to argue that the explicit requirement for some kind of competitive (or similar) interaction should be explicitly added to standard accounts of selection. A mild version of this position is espoused by Godfrey-Smith (2009), who requires competitive interaction for a case of selection to be regarded as a full-blooded "paradigm" instance. The most extreme form might be associated with Van Valen (1973, 1975 and discussed in chapter four), who unflinchingly recasts all of selective theory in terms of resource competition, with fairly sweeping implications.

5.9. Insistence on Competition

To reject "non-interactive" scenarios like Lewontin's Bacteria risks throwing the baby out with the bathwater, in that it requires the rejection of what seem to be clear "paradigm" cases of selection[5]. To take an example, let us imagine the effect of a very harsh winter on a population of animals. The group contains two types – X and Y – each with 100 individuals initially present. Let us say X proves to be more vulnerable to the cold than Y. After winter has run its course, only 40 Xs and 80 Ys remain, the rest having frozen to death. Few would argue that the differential survival of types here represents anything other than a clear case of selection in action, which very much accords with our intuitions.

Nevertheless, this is not a case of competition as I have defined it, as there is no zero-sum contest over any resource, such as food or mates. Under competitive circumstances, success will inherently come at the expense of others, and we would expect to see individuals selected according to how their traits compare *relative* to one another. If there were a competition for cold tolerance – perhaps individuals win some resource contest by surviving in cold conditions for the longest period of time – then we would expect to see success simply as a function only of how an individual's tolerance ranked against its competitors. Thus, the *most* cold-tolerant individuals would be the victors, whether they survived the cold for five minutes or five hours – as long as this was *longer* than their competitors. In our example here, though, individuals have been selected according to their *absolute*, rather than relative, ability to withstand weather conditions. Had all been highly cold-tolerant, all could have survived winter, with the survival of one not preventing the survival of others. By the same token, there were no cooperative

[5] Readers worried about the other side of the coin here – that removing competition as a necessity allows us too readily to declare entities under selection together – should refer to chapter six, section one, where I show that competition is not tenable as a means of defining Darwinian populations.

or exploitative interactions between the animals or any other organisms (predators, for example). Thus, this is a clear example of selection with no salient interactions between individuals *at all*.

If we were to add some explicit requirement for competition or similar causal interaction between members of a Darwinian population to the schematic criteria for selection, then we would immediately rule out such cases of selection at the hands of harsh weather conditions and many others besides. Getting rid of "non-interactive" selection, then, might satisfy *some* intuitions about Lewontin's Bacteria, but would go *entirely* against our intuitions regarding this case of the freezing animals. That said, trying to weigh the value of these intuitions against one another is perhaps as much of a fool's errand as trying to derive one's selective theory entirely from those intuitions in the first instance.

Beyond the vagaries of intuition, though, there is a more objective reason to regard non-interactive cases as selective. Specifically, this is the fact that these scenarios are amenable to highly meaningful selective explanations. Even in the apparently controversial case of Lewontin's Bacteria, a biologist might very well be interested to give a selective explanation for why their vessel is filled with much more of the faster-growing strain than the slower. Thus, they might state that the more numerous strain reproduced faster by virtue of being better adapted to the prevailing conditions. Certainly, we would also wish to give selective explanations when variants exhibit differential survival in harsh environmental conditions, as in the winter survival example I have just given. If we were to insist that these scenarios are not selective for want of competition or some similar interaction, we would sacrifice the ability to make such explanations across vast swathes of cases.

As per my remarks in previous sections, and contrary to Godfrey-Smith's requirement for competition, selection in such cases can also be relevant to origin explanations. If our animals happen to be sexual reproducers, then the effect of differential environmental interaction on the relative abundance of types will also influence the likelihood of different genotypes coming into existence in future generations. For example, the increased vulnerability of the Xs means that there is less chance of their alleles combining with genes from the population of Ys and more chance of Ys breeding with one another. As such, this is a potentially creative instance of selection, capable of generating origin as well as distribution explanations.

It could be argued that the presence of sexual reproduction constitutes a significant causal interaction between individuals in itself. Indeed, under Godfrey-Smith's account, this causal linkage would at least move a scenario in the direction of being a paradigm case of selection. It might then be thought that this fact somehow "excuses" this class of examples from counting against Godfrey-Smith by differentiating them from more austere cases like Lewontin's Bacteria. However, I do not think that this approach

represents the relevant causality here. No doubt sexual reproduction constitutes a causal link between the individuals under selection. However, it does not follow that that linkage will actually be relevant to the action of selection in any way. In competitive selection, the competitive causal linkage between individuals is what drives selection – success and failure in competition simply *is* selection in such cases. If, in other scenarios, selection really does act as a function only of how individuals relate to their environments, other facts about those individuals are not particularly salient to how we think about that instance of selection. Thus, if animals simply freeze to death in winter, I do not see that their particular method of reproduction should determine how we think about what happened to the frozen animals any more so than whether they were herbivorous or carnivorous, or oviparous or viviparous. In this kind of scenario, reproduction might provide a causal linkage between individuals, but not one that is relevant to the immediate action of selection.

6. A New Taxonomy of Selection

All these points provide a compelling case to accept "non-interactive" scenarios, such as Lewontin's Bacteria, as valid instances of selection – in spite of any intuitions to the contrary. Importantly, though, it is entirely possible to accept such cases as selective whilst also recognising that they can differ significantly from instances of selection driven by competition and other interactions between individuals.

The idea that there are different forms of selection depending upon different causal relations between the individuals involved sounds rather like the taxonomy of selection put forward by Godfrey-Smith. However, my own proposed taxonomy differs significantly. As mentioned above, Godfrey-Smith (2009) distinguishes between "minimal" and "paradigm" cases of selection, placing a spectrum of intermediate cases between them. The presence of sexual reproduction pushes a case along the scale toward being a paradigm one, but competition is taken to be essential for a true paradigm case due to its asserted unique relevance to origin explanations.

Godfrey-Smith's account makes reference only to competition, and not to cooperation or exploitation. By contrast, I wish to recognise cooperation and exploitation as distinct and important drivers of selection besides competition. Indeed, I have shown that cooperative and exploitative selection can have very similar results and that – by Godfrey-Smith's own reasoning – cooperation and exploitation can actually be *more* clearly relevant to origin explanation (via increasing absolute numbers of successful types) than competition.

My taxonomy centres on a division between two basic forms of selection. To make my proposed differentiation as clear as possible, I will borrow some terminology from game theory. Thus, I wish to categorise selection driven by directly relevant causal interactions between individuals – that is, with non-zero alpha values as discussed above – as different modes of "strategic" selection. Accordingly, the category of strategic selection will include and be subdivided into the sub-categories of competitive, cooperative and exploitative selection. Besides strategic forms of selection, I wish to categorise all those examples of selection lacking any directly relevant causal interaction between members of the Darwinian population – those where all alpha values equal zero – as cases of "parametric" selection. I avoid the terms "interactive" and "non-interactive", despite my shorthand usage above, as they might generate confusion by suggesting there is no interaction with the environment – which, of course, there always is – and also because the existing game-theoretic differentiation maps so well onto the phenomena I wish to describe.

We have explored the differences in character between these two kinds of selection in some detail. However, it will be important for future development to stress that both are aspects of what is fundamentally the same process. We should bear in mind that, at any instantaneous moment in time, at the level of the individual, the two forms of selection are effectively identical. In both cases, each entity will have an expected reproductive rate or fitness as a function of the prevailing environment – where that environment will include the state of any peers it is interacting with. The important difference between the two kinds of selection, then, is simply that, in the parametric case, the environment is fixed insofar as it does not respond to the behaviour of the focal entity whereas, in the strategic case, the environment can subsequently vary over time in response to the focal entity's actions. The difference between the modes of strategic selection, such as between competition and cooperation, is just the particular way in which those changes then occur.

Mapping Godfrey-Smith's taxonomy onto my own, his paradigm cases of selection will be a subset of competitive selection (itself a subset of strategic selection) where sexual reproduction is in operation. His minimal cases of selection would be a subset of parametric selection where no sexual reproduction is present. Based on my points here, I think that we should ascribe more equal importance to parametric and strategic selection than does Godfrey-Smith for his paradigm and minimal categories. Harsh environments can make parametric selection very powerful. In addition, some life forms seem to be primarily subject to parametric selection and are specifically adapted to meet its requirements. For example, "r-selected" species (MacArthur and Wilson 1967, Pianka 1970) are adapted to produce the maximal number of offspring possible in their general environment, as the areas they inhabit are sufficiently harsh and/or changeable that their niche never reaches carrying capacity – so zero-sum competition never gets started. Crucially, we have also seen that both strategic and parametric forms of

selection can be relevant to origin explanations, undermining the rationale by which Godfrey-Smith justifies his hierarchy.

7. Attempts to Partition Parametric Selection

Near the beginning of this chapter, I noted that some authors have attempted to put forward non-competitive accounts of struggle. These become relevant here, as they notionally provide a means for those sceptical of my taxonomy to partition my category of parametric selection so as to exclude less intuitive cases, such as Lewontin's Bacteria, as instances of selection.

Lennox and Wilson (1994) develop their own idea of non-competitive struggle, precisely with the intention of ruling out such cases as selective. If theirs or a similar account could be sustained, it would undercut my argument that we must accept the whole category of parametric selection, including apparently counter-intuitive cases, on penalty on losing out on selective explanations for intuitive cases – such as my freezing animals, above.

However, as I also noted earlier, these non-competitive accounts of struggle are not tenable. Lennox and Wilson rely on being able to specify the absolutely optimal set of conditions for an individual or type, with the idea that entities experiencing sub-optimal conditions can be said to struggle as a result. Ostensibly, this seems intuitive enough, capturing the non-competitive sense of struggle I noted in section one (whereby I would struggle to run 26 miles, even if not in a race). However, it is less than clear how this mode of struggle can be defined in practice. This is especially so, considering that more favourable conditions might be created in a lab than would be available anywhere in the natural world. Should we take these artificial conditions to be optimal or limit our consideration to naturally available environments? What about conditions that might occur naturally, but with a vanishingly low probability? This brings us to the standard problems of the tractability of assessing competing counterfactuals (Weatherson 2016), already discussed in relation to Godfrey-Smith's position on competition. The result is that it is impossible to claim that we can know *absolutely* whether an entity is engaged in struggle or not, as defined by Lennox and Wilson. Generally, any non-competitive account of struggle (such as might partition my category of parametric selection) seems doomed to collapse to an unavoidably subjective judgement as to whether conditions are harsh – entailing struggle – or benign – with organisms not struggling.

Without sufficient space to offer a fully detailed analysis of non-competitive accounts of struggle, my remarks here must suffice to show my awareness of such theories and provide a brief outline of why I

do not think they are feasible. In any case, whether such accounts could be made to work or not does nothing to diminish the other half of my argument for accepting the full set of parametric cases of selection. That is that all such cases, including those like Lewontin's Bacteria, can be the subject of perfectly interesting, valid cases of selective explanation, such that a theory of natural selection that cannot recognise them will be unacceptably impoverished as a result.

Conclusion

I have used this chapter to explore the role of struggle in natural selection, where struggle is thought of in terms of zero-sum competition. I agreed with Godfrey-Smith that there were many important special features of competitive selection and spent some time discussing them. However, I also noted that selection based on other kinds of interaction between individuals manifested analogous features.

Godfrey-Smith emphasises the role of competition, claiming it uniquely allows for selection to offer origin explanations as to the emergence of new adaptations. However, I showed that Godfrey-Smith's route to these explanations necessarily includes an inherently subjective counterfactual judgement. By contrast, I demonstrated that instances of selection driven by cooperative and exploitative interactions are actually better candidates in allowing for objective origin explanations. Indeed, I developed ideas from Neander to show that origin explanations are possible even where selection is driven simply by interaction with the abiotic environment, so long as sexual reproduction (or similar) is present.

In light of all this, I proposed a new taxonomy of selection to replace that offered by Godfrey-Smith. Thus, I divide cases of selection into two broad groups. Strategic selection can be driven by competition as well as by cooperation or exploitation between individuals. Parametric selection is driven simply by interaction with the general environment. Whereas Godfrey-Smith ascribes significant priority to competitive cases within his group of paradigm instances of selection, I think we would profit from seeing strategic and parametric forms of selection as something closer to equivalent categories. I emphasise that parametric selection can be very powerful in itself and can yield origin explanations, giving it a role in adaptation. I also note that, in some cases – such as for r-selected species – this might be the dominant form of selection affecting a population.

My category of parametric selection also includes apparently counter-intuitive cases like Lewontin's Bacteria, which some will find difficult to accept as true instances of natural selection. Lennox and Wilson seek to rule out less intuitive cases of parametric selection by developing a non-competitive

idea of struggle. However, I briefly demonstrated that such accounts will run into serious conceptual issues.

At several points in this chapter, I have discussed selection driven by interactions between members of more than one species. Since selection is typically taken to occur between conspecifics, some readers might object to my points via appeal to a strictly single-species Darwinian population concept. Other readers might worry generally that removing the requirement for competition between those under selection is far too permissive in allowing us to declare entities under selection together. To address these and other points arising in subsequent chapters, I conduct a thorough discussion on defining the Darwinian population in chapter six.

Similarly, if we had previously thought about selection as something like a competition to contribute offspring to the next generation, then we might have considered biological fitness to be some function of success (whether expected or realised) in such a competition. Removing the necessity for competition thus invites us to question how we think about fitness in general. As such, in the subsequent four chapters, I will analyse our most fundamental commitments around fitness, demonstrating problems with our current picture and suggesting alternative directions to rectify these.

II

FITNESS METRIC PLURALISM

In the previous chapter, I examined the common assumption that struggle in the form of zero-sum competition is a necessary component of natural selection. I found that there was no necessity for causal linkage between individuals under selection and that, where such linkage was present, it might be of a character other than competitive. In the course of discussion, there were moments where challenging the status of competition in selection seemed to raise questions for how we think about fitness. As we would expect for any theory, the foundational concepts of our account of natural selection mutually underpin one another. Thus, when we destabilise one such central concept, we will cause problems for others.

Our understanding of biological fitness is as coloured by uninspected assumptions as our ideas about the role of competition in selection. Thus, across this and the subsequent three chapters, I will present an analysis of biological success. I will begin from an inspection of some of the rarely challenged commitments which underpin much of our theory of fitness. Initial criticism will present an opportunity to develop a more capable account, eventually allowing for significant expansion in the explanatory scope of selective theory in general.

Fitness is often conceived of as reflective of success in some competition to contribute offspring (or tokens of some gene or trait type) to the next generation. We have already undermined the idea that competition need be present. In the chapter following this one, I will turn my attention to the idea that the relevant time frame is of the order of a single generation. Here, though, I will commence my analysis of fitness by addressing our most basic commitment in any account of that concept. This is the quantity in terms of which fitness is taken to be measured.

The main sections of this chapter will be structured as follows:

1. Foundations – Defining Terms

To begin, I explain that mainstream accounts of fitness, regardless of other points of difference, are generally committed to measuring biological success in terms of some function of number

of entities – whether that means counting the number of individuals, offspring, gene tokens or otherwise. I refer to such standard treatments as “numerosity” accounts.

To more clearly define my target for analysis, I set up a terminological distinction between fitness “metrics”, “measurement schemes” and “concepts”. These terms denote components of any theory of fitness and will form a useful shorthand, across this and subsequent chapters, to refer to distinct levels of analysis. Making this distinction, particularly between fitness metric and measurement scheme, allows me to explain that my points here will not directly impinge on the major controversies in the contemporary fitness literature, which occur logically downstream of commitment to a particular fitness metric.

2. Problems for the Numerosity Approach

Commencing the main discussion, I rehearse some relatively well-known examples that are problematic for numerosity accounts of fitness. We see that, outside of the realm of "familiar" species, biological success is often manifested in terms of quantities including biomass and persistence, rather than in terms of numerosity.

3. Possible Responses to Problems With the Numerosity Approach

I explore several possible responses to such problematic cases. Thus, I find it is impossible either to stick to a pure numerosity-based metric, or to switch to a similar, monist account based on an alternative metric, without losing the ability to offer selective explanations for some subset of ostensibly selective scenarios. As such, I recommend we adopt a pluralist approach to fitness measurement, allowing selective explanations in terms of different metrics as appropriate to different scenarios and even to describe the same case using multiple metrics simultaneously. Notably, this conclusion is provisional on no unifying “common currency” metric being available. Since none are present in the mainstream literature, I defer full investigation of this idea until chapters four and five.

4. Implications of a Pluralist Approach

A pluralist approach allows us to capture selection in terms of all valid metrics, avoiding any problem of “information loss”. Thus, metric pluralism promises a significant expansion in the explanatory scope of our theory of natural selection. Rather than perceive this shift to pluralism as a retreat from parsimonious theory, I argue that our initial monist position was never actually warranted.

A pluralist account means that we will no longer necessarily be able to generate absolute fitness rankings. However, I note that, in familiar cases where the standard numerosity approach was already satisfactory, such rankings will generally still be possible. I also provide brief comments on how a pluralist stance on fitness could be of significant utility in efforts to extend selective explanations both to non-standard levels of selection and substrates, such as clade selection cultural selection. Overall, significant expansion in the scope of selective explanation more than balances any perceived downside for pluralism.

Finally, I note that a pluralist approach to fitness measurement does raise broader conceptual questions. Particularly, allowing for multiple fitness metrics begs the question as to what distinguishes valid from invalid metrics. Thus, I return to address this issue, along with the related idea of deriving a common currency fitness metric in chapters four and five.

Concluding, I explain that, in the next chapter, I will extend this generally pluralist approach to the measurement of fitness over time.

1. Foundations

Before delving into the main discussion, I will set the content of this chapter in context and clarify what I take key terms to mean. Much of the content in this section will be equally relevant to subsequent chapters to this one.

1.1. The Conventional Approach – "Numerosity"

It hardly needs to be stated that there is an enormous literature – full of disparate schools of thought – across many aspects of selection in general and biological fitness in particular (Rosenberg and Bouchard 2015). However, despite all their points of difference, mainstream accounts are united in a fundamental idea that fitness is some function of what I will call "numerosity".

By "numerosity", I mean that fitness values will be arrived at as some function of *counting* the number of elements of some set of entities. Depending on the specific account of fitness, this might mean counting the number of a certain type or the number (or indeed mean number) of offspring or copies produced, either by a type or a focal individual. Inclusive fitness (associated with Hamilton 1964) adds subtlety with the idea of counting fractions of individuals according to their relatedness. What is shared is that it is simply the *number* of these entities themselves that is attended to across conventional accounts of fitness, rather than any of their other qualities (such as somatic size or lifespan).

Now, to be as clear as possible, with the idea of "numerosity", I am *not* referring simply to the practice of generating *numerical* fitness values. Even if we discarded a numerosity approach where, say, we counted the number of offspring of a lineage in favour of, say, a biomass-based metric where we examined the total mass of all the members of a lineage, the new fitness values would still be numerical figures (presumably denominated in kilograms or similar). However, we would have transitioned away from a "numerosity" approach as I have defined it, as we would no longer be thinking about fitness in terms of the number of elements of some set of entities.

It is worth noting that this numerosity approach seems to rest on an underlying, implicit assumption that the entities being counted are sufficiently similar such that the only meaningful dimension of salient variation will be the number of these equivalent units. This assumption is clearly more immediately plausible for gene copies than individual organisms but seems to be applied in blanket fashion regardless. Thus, just as a parent presenting their child with a handful of identical red blocks will struggle to find a better educational question to ask than "how many?", so the numerosity approach seems to ask us to regard the biological entities within a Darwinian population as similarly equivalent. As will be seen in section two, the shortcomings of the numerosity approach are exposed precisely where there is significant disparity between individuals.

In practice then, disagreements in the literature between rival accounts of fitness are logically downstream of this shared, foundational commitment to a numerosity approach. Discussion has focussed on questions as to what *kind* of entities we should be counting and *how* exactly we ought to go about counting them. Thus, we have the well-known debates over levels of selection - particularly over whether the basic units we should be counting ought to be gene copies or individual organisms (Lloyd 2020). Similarly, we see ongoing discussion as to whether fitness values should purely reflect "realised" numbers of entities counted retrospectively or whether values should encode expected future numerosity as a "propensity" of different types (Mills and Beatty 1979). However, authors across these debates (almost) universally operate within this "conventional" consensus, in that wherever and however they say fitness should be measured, this is always to be done as some function of numerosity.

In fact, even the most dissident accounts of fitness amongst the contemporary literature will generally refer back to numerosity. For example, even Bouchard's (2008) account of ecological fitness – contributing to a tradition seeking to re-conceptualise fitness in terms of direct assessment of adaptation to the prevailing environment – defaults back to recommending a numerosity approach in terms of actual measurement.

It is perfectly reasonable that these and similar discussions have been the subject of large bodies of work, as authors seek to elaborate the numerosity account. Indeed, as the next sub-section will make clear, many of these logically downstream issues would be just as live even if we exchanged a numerosity metric for an alternative. In short, this is valuable work. However, for our purposes here, all of the various positions within the mainstream literature can be taken as only superficially distinct iterations of the same conventional "numerosity" approach to fitness; united by a foundational consensus on fitness being a matter of the number of some set of entities.

1.2. Levels of Analysis – Fitness Metric, Measurement Scheme and Concept

The job of this chapter, then, is to begin to challenge this general consensus. Doing so will mean operating at a level of analysis logically prior to the mainstream fitness literature. Indeed, it will be useful – here and in subsequent chapters – to have some explicit terminology by which to separate the relevant levels of analysis. As such, I will employ an approximate, tripartite distinction between fitness "metric", "measurement scheme" and "concept", as three key elements which will be contained within any overall account of fitness. By setting out this distinction, I can also more clearly define the bounds of what I will be discussing here.

1.2.1. Metric

In this chapter, I will be concerned exclusively with the question of which metric, or metrics, we should employ to measure fitness. This is the question of which *quantity* fitness should be measured in terms of. The conventional approach, characterised above, measures fitness as some function of number of entities. In subsequent sections here, I will also examine ideas of measuring fitness as a function of biomass or persistence over time. In later chapters, I will go on to explore the possibility of assessing fitness in terms of energy or resource consumption, as well as more exotic quantities.

Choosing a specific fitness metric can be thought of as the first step to assembling a complete theory of fitness. However, just knowing the quantity in which we wish to denominate fitness does not take us very far in itself. We will still need to know how to go from empirical observations to final values and to have an idea as to how those values are meaningful. This is where our fitness "measurement scheme" and "concept" respectively enter play.

1.2.2. Measurement Scheme

Whichever fitness metric we decide upon will be employed within a wider "measurement scheme". This dictates the method by which we move from empirical data to then generate fitness values in terms of that chosen metric. A ready example here is the propensity account

put forward by Mills and Beatty (1979), which moves from data on reproductive success to generate a fitness value as an expected future reproductive output.

Measurement scheme and metric are largely separable from one another and the same metric can be employed within very different measurement schemes. Thus, we see debate between different ways of constructing propensity approaches (Beatty and Finsen 1989) and much more pronounced differences in how fitness values are arrived at between propensity accounts of any shade and their rivals in the statisticalist tradition. However, all of these accounts remain fundamentally committed to a numerosity metric.

The great majority of modern literature on fitness is concerned with working out details at the level of the measurement scheme. For instance, the debate around the validity of the propensity approach generally takes for granted that fitness values will be in terms of number, focussing instead on the specifics of how numerosity-based values should be calculated. In particular, within work on the propensity approach, there is a substantial body of literature as to the specifics of how to take account of differences in qualities like variance and skew in the offspring probability distributions used to generate expected fitness values (as per Sober 2001, Beatty and Finsen 1989, Gillespie 1977 and discussed in chapter three). Often, work at this level will be highly technical. Grafen (2014 for an outline), in particular, produces very mathematically involved arguments as to the specifics of numerosity-based fitness measurement. Once again, though all this work occurs logically downstream from the adoption of a numerosity approach.

However, just as the same fitness metric can be employed in multiple different measurement schemes, so the same broad measurement scheme can potentially be compatible with multiple different metrics. For example, Cooper (1984), in setting out his Expected Time to Extinction (ETE) measure, takes a propensity approach to fitness with a similar structure to that of Mills and Beatty but substitutes the standard numerosity metric with one of persistence. Cooper's account thus effectively generates fitness values as a propensity to persist rather than a propensity to reproduce.

Testament to the separability of metric and measurement scheme, Krimbas (2004) also develops a pluralist approach to fitness but at an entirely separate level of analysis to the pluralist account I will elaborate in this chapter. Krimbas is exclusively concerned with fitness measured in terms of numerosity and concludes that any one way of measuring fitness within that framework will fail to function properly across all the cases to which it might be applied.

In my terminology, Krimbas claims that any one measurement scheme will be unsatisfactory in elaborating a numerosity-based account of fitness. Indeed, many of his points (for example, where success after one generation does not predict success in later generations) might be equally problematic where fitness was quantified in terms of another metric. However, his work is logically downstream of the basic choice of which metric to employ.

Generally, this separability of metric and measurement scheme means that my work in this chapter on fitness metrics is logically separable from debate around measurement schemes. Happily, this removes the need for tangents into other areas of the literature and generally makes our task here a more contained and tractable one.

1.2.3. Concept

Finally, I will use the term "fitness concept" to refer to the broad theoretical framework - the general theory of fitness – which ultimately accords meaning to the value produced by the measurement scheme. The fitness concept will determine the metric used and at least the general form of the measurement scheme. However, it is possible to make use of the same fitness metric and measurement scheme, whilst interpreting the results within a very different fitness concept. Thus, at the level of metric and measurement scheme, Williams (1970) sets out a very conventional account of fitness as a function of number of individuals, but then takes the more unusual conceptual approach of regarding number-based fitness values merely as a guide to, or proxy for, the persistence of types/lineages – which she regards as corresponding to the fundamental nature of fitness. By contrast, Mills and Beatty (1979) regard their numerosity-based propensity approach as a proxy for how "well designed" an individual is for its environment. Thoday (1953) elaborates a theory of fitness as a multi-faceted phenomenon, conceptually similar to the account I will put forward here. However, at total variance to my metric-pluralist approach, Thoday argues that making a single, persistence-based measure is the best way to capture fitness so-conceived.

The idea of a fitness concept can become somewhat redundant or invisible in some strains of mainstream thought, where a strict numerosity approach is taken at all levels. Thus, where fitness is measured simply in terms of number of entities – and this alone is considered the entire fact of biological success – fitness metric, concept and even measurement scheme largely collapse into one another. However, going forward with our analysis, distinguishing these different levels as to how we deal with fitness becomes increasingly important. In particular, as I will discuss in a later section, moving from a monist to pluralist approach to fitness

measurement will necessitate some change to our overall fitness concept. This is an issue I will address later here and also in chapters four and five.

2. Problem Cases

Despite the consensus in considering fitness in terms of numerosity, there are well-known examples of real-world cases where this metric fails to capture apparently valid instances of selection. In such scenarios, selection seems to favour biological success in terms of quantities other than the number of any set of entities. If we wish to offer selective explanations for these scenarios, we must measure fitness in terms of other quantities. Here, I will consider examples where fitness appears to be expressed in terms of somatic growth and persistence, before considering the implications of such cases.

These scenarios will tend to be instances where the tacitly assumed equivalence between entities counted by a numerosity account breaks down. Where entities are effectively identical, any of the metrics we might be interested in will strongly covary with the others. Thus, for most "familiar" species, where conspecifics are relatively similar to one another, the reproductive success of a lineage will very closely track that lineage's total biomass and the time for which it can be expected to persist. In such cases, it hardly matters which metric we track, as we will emerge with a very similar picture of selective dynamics. However, when we are confronted with cases where success appears to have been in terms of quantities that do not covary with the number of any set of entities, the numerosity approach seems to obscure selective reality. Eventually, then, we are left with the question – to which I will return in section 4.4 – as to what initial justification we ever really had to make numerosity our exclusive focus in appreciating selection.

2.1. Growth

The go-to example of selection in terms of somatic growth is that of the giant fungi of the *Armillaria* genus, which includes the famous *Armillaria gallica* "humungous" fungus. This group of species provides an illustration of organisms that manifest biological success not by increasing in number, but by increasing in size. Thus, very large sizes can be achieved, with single individuals weighing in at over 100 tons (Casselman 2007).

Where differential growth occurs because of a difference in level of adaptation to the prevailing conditions, it seems reasonable that we should be able to offer a selective explanation of what we observe. Thus, we might wish to regard the relatively larger biomass of a well-adapted variant compared to a poorly adapted, smaller strain as an expression of a difference in fitness between the two types.

However, a conventional approach to fitness will not register differences in biomass where they are not accompanied by changes in numerosity. Thus, one individual will count equally to its neighbour, even if it grows to one thousand times the size of that neighbour. Number is all that matters. As such, it seems that numerosity-based fitness fails in allowing for us to provide a valid selective explanation.

Armillaria gallica already provides a good example of selection where fitness is better denominated in terms of somatic growth than in offspring number. However, with such a strong consensus around seeing fitness in terms of numerosity, there will likely be a subset of readers who simply reject this idea out of hand. To help bring such readers with my line of reasoning, we can perhaps provide an even clearer illustration of why we should be willing to conceive of selection and fitness in terms of somatic growth by taking a case where the distinction between reproduction and growth is ambiguous, but where selection clearly acts regardless. Thus, we will consider another stock example in the form of the quaking aspen.

The quaking aspen is a species of tree that appears to grow in normal groups or forests of individual trees, as with familiar species. However, the aspen is actually quite different. Rather than any new sapling we see above ground having grown from a sexually derived seed, in most cases that sapling will in fact be the offshoot of an underground runner emanating from an established plant. Unlike some plant species, the runners giving rise to new Aspen "trees" do not disintegrate to leave physically isolated individuals, nor does their adaptive role end with establishing a new stem above ground. Rather, in aspen, runners are maintained and develop to form a highly integrated root system, which can provision younger or struggling trees and thus actively facilitate the exploration of new areas. The resulting giant organism is called a “grove” and can grow to enormous sizes (Clarke 2010, 2011, 2012, Bouchard 2008).

When we observe the differential spread of two aspen groves above ground, it will look very much as if we were watching the differential reproduction of two types within a more typical species. To make matters more complex, sometimes events lead to the fragmentation of the root system, leaving us with no reliable means of telling above ground whether any one "tree" is a free-living individual or part of a larger grove. When we add this ambiguity as to which "trees" are connected to the larger groves, we will struggle even further to perceive any obvious difference in observational phenomena between selection by numerosity and by somatic growth (Bouchard 2008).

Aspen make use of growth by runner as a quicker means to occupy new space or to replace a dead trunk than would be possible by seeding, allowing them to outpace members of other species in competition for land. Not only do runners allow new space to be reached first, but being provisioned by the

integrated root system will mean that the new stem in that location can grow at an accelerated pace, so as to minimise the chance of being eaten by herbivores. Thus, there is good biological reason for aspen to prioritise growth over reproduction.

Where one strain of aspen spreads faster than another in the same environment, or where one strain competitively displaces another, it seems we should be able to offer a selective explanation regardless of whether the trunks of each aspen strain turn out to be physically distinct individuals, parts of the same physically integrated grove or some combination of the two. Where we observe the same characteristic behaviours, it would seem perverse to then limit valid cases of selection to those where we had gone digging to establish the separation of root systems. In this context, we can see that numerosity-based fitness perhaps presupposes rather neater distinctions between individuals than we actually find in nature. For the aspen, then, it seems sensible to offer a selective explanation of our observations in terms of biomass, as this appears to be the quantity that selection is acting upon regardless of how questions of individuality play out.

2.1.1. A Response on Behalf of Numerosity Accounts - "Chunking"

Selection amongst the quaking aspen is also a useful case in illustrating a possible objection to the idea that we need to move away from a numerosity metric to capture biological success in terms of somatic growth. The idea is that, in such scenarios, we should be able to identify a means of tracking change in biomass in terms of numerosity, even if this means shifting the level of organisation at which we do our counting. Thus, whilst one might debate their status as biological individuals (Clarke 2011, Wilson and Barker 2019), the number of trunks in an aspen grove can be expected to track the biomass of that grove, as the trunks will each be of roughly equivalent mass. Generally, then, it seems we might retain a numerosity approach to fitness whilst tracking biomass by counting the roughly equivalent modular units which increase in number as entities grow. This "chunking" strategy (as I refer to it here), is similar to that put forward by Bouchard (2008) and Gill and Halverson (1984).

In nature, we do typically find that larger individuals are made up of assemblages of smaller, modular parts. Just as a familiar organism is made up of many cells, so an aspen grove is made up of many trunks, the super-organism of an ant colony is made up of many ants and so on. We can indeed expect a chunking strategy to function in many such cases, where increase in size will mean adding more modular parts. However, there is no guarantee that growth will *universally* be a matter of the proliferation of modular components. Take the realm of single-celled organisms, for instance (which we should remember makes up a huge fraction of life on earth, whether in terms of variety or biomass – as per Bar-On, Phillips and Milo 2018). Contrary

to popular imagination, single-celled organisms come in a wide variety of sizes. The mono-cellular algae *Caulerpa taxifolia* reaches a full size of one foot in length, having convergently developed marine analogues of many structures found in multicellular terrestrial plants, but hosted within a single cell (Meinesz et al 1995). Growth by such an individual cannot be reduced to a matter of adding modular units. As such, we cannot rely on "chunking" strategies to provide a universal means of accommodating selection in terms of somatic size within a numerosity approach to fitness and should be prepared to measure fitness as a direct function of biomass.

On a less rigorous note, we can expect that there will be many cases where applying such a "chunking" strategy will seem incredibly arbitrary and ad hoc. If we have to descend to the microscopic level of cells in order to find something to count rather than weigh, it will look very much as if the principle of selection in terms of growth has already been conceded; with our taking such steps purely in order to retain a now-hollow commitment to a numerosity-based metric. If we wish to accommodate selection in terms of somatic growth, it is surely more honest to simply do so directly, in terms of biomass, rather than resort to the theoretical equivalent of creative accounting.

2.2. Persistence

The idea of survival as a central phenomenon within natural selection goes all the way back to Darwin, and it has been common to cite survival as an important component of fitness since those earliest days of evolutionary theory, right through to the present era. Indeed, a standard numerosity account will already allow for some instances of selection on survival. To take an example, let us imagine a population of organisms that is divided between two strains - A and B - existing in equal numbers of, say, 50 each. Now let us imagine the whole population is exposed to a new pathogen outside of the breeding season. It turns out that B copes with the new affliction better than A, so that, after the outbreak has run its course, individuals of each type have died. However, more of A have perished than B so that now there are 20 of A and 35 of B. As such, we see a changing relative frequency of variants as a result of differential adaptiveness of traits, in just the same manner as we might had reproduction mediated that change. Most observers would thus be content to say that we had witnessed selection in action here, without waiting until breeding season to observe the resulting composition of a future generation. Indeed, Endler (1986) records similar treatments of fitness measurement in empirical scientific studies.

We might think that this ability to include selection for survival as a kind of limiting case means that standard treatments of fitness can account for persistence generally. In many cases, numerosity and persistence accounts will indeed converge. However, in cases where the equivalence of individuals

again breaks down and we see significant variation in individual longevity, we can start to see selection via differences in that variable.

There is some history of attempts to conceptualise fitness in terms of the persistence of lineages (Thoday 1953, Cooper 1984, Bouchard 2008). In defending his own persistence-based account of fitness, Bouchard (2008) also cites the cases of *Armillaria gallica* and the quaking aspen. However, he uses the incredibly long lifespans of the organisms to make his point in the same manner as I have used their great biomass. Scenarios where fitness is realised in terms of persistence are not limited to entities capable of accruing mass by vegetative growth, though. We might look here to the famous, biologically immortal species of jellyfish *Turritopsis dohrnii*, which I will discuss below in section 3.2.2. As a similar example, Bouchard (2008) discusses selection amongst ant colonies, where we can expect the total size of physical nest structures to be capped in absolute terms by engineering concerns regarding material properties and the rate at which gases can be diffused (see Turner 2007 on the relevant engineering constraints and on colony-level selection).

In such cases, numerosity will not give any indication as to vast possible differences in lifespan. One aspen grove or immortal jellyfish might last a few years or centuries – simply knowing that there is *one* such organism will not tell us which will be the case. Thus, if we wish to offer selective explanations for differences in persistence, we cannot do so in terms of numerosity.

3. Possible Responses to Problems With the Numerosity Approach

We have seen that there are cases where it seems appropriate to offer selective explanations, but where we would need to make use of metrics other than numerosity to do so. Going forward, there are four routes open to us. I will survey each in turn, arriving at my own account as the fourth option.

3.1. Stick with Numerosity Regardless

The received view of selection is founded on an assumption that numerosity is the single valid quantity by which to measure fitness. One way to proceed in light of the cases we have seen is to simply retain this assumption and work around it. There is indeed some capacity for a numerosity approach to account for selection in terms of somatic growth. I have noted how the "chunking" strategies discussed by Bouchard (2008) and Gill and Halverson (1984) might account for some variance in biomass via the numerosity of similarly sized modular parts. Thus, we might count the trunks in an aspen grove as a proxy for biomass. As we have also noted, though, the possibility that entities might grow other than

by adding modular units (including single-celled entities) means that "chunking" strategies will not always be applicable to cases of selection where fitness is manifested in terms of somatic growth.

By the same token, ideas like that of reproductive value (described by Fisher 1930, developed in some depth by Grafen 2006 and discussed in the next chapter) might be able to assign some weighting to numerosity measures, so as to take account of the persistence of lineages over multiple generations. Reproductive value weights offspring in terms of the number of subsequent offspring they are then likely to produce themselves. This allows the future life expectancy of a lineage to inform a standard fitness measure to some degree. Again, though, the utility of such a strategy will be limited. For instance, reproductive value still ultimately functions in terms of numerosity of individuals and will only track persistence as a sum of the roughly equivalent lifespans of such individuals over a lineage. As such, reproductive value would have a limited capacity to capture significant differences in individual lifespans - the kind of case where we might wish to perceive selection on longevity within a single generation, without examining reproduction at all. Thus, the idea of reproductive value will not help us extend a numerosity-based account of fitness to allow for selective explanations of differences in longevity of individual aspen, *Turritopsis dohrnii* or *Armillaria gallica*.

Even with all possible modifications and additions we might make, retaining a monist, numerosity-based fitness metric will inherently mean failing to account for a subset of ostensibly valid cases of selection. It does not seem tenable to simply ignore this set of cases or to rule them out of consideration by arbitrary fiat. As such, some justification must be provided for why we are not willing to accommodate these scenarios within our theory of fitness. I will consider the most obvious putative justification before proceeding further.

3.1.1. Dawkins' Criterion

Any justification for sticking to a monist numerosity approach to fitness – despite this implying failure to explain selection in terms of other quantities – must provide a rationale for why we ought to be concerned only with the set of cases amenable to description in terms of numerosity. That is to say, to be able to stick to a pure numerosity approach, we need to explain why problematic cases are not valid or relevant instances of selection.

Based on the existing literature, the most likely way to take this approach would be to apply Dawkins' argument (2016, with the same ideas discussed with more nuance in Godfrey-Smith 2009) as to the particular importance of reproduction for selection. Briefly, Dawkins' claim is that reproduction, as defined by a single-cell bottleneck, is essential in allowing for the evolution of complex adaptation, as only the re-starting of development necessitated by such a

bottleneck can allow for large-scale organisational changes in phenotype. The idea, then, is that only cases which can lead to complex adaptation are worthy of consideration as meaningful instances of selection. Applying what I will call "Dawkins' Criterion", thus restricts the set of valid cases of selection to those containing appropriately bottlenecked reproduction - which is, in turn, a set of cases that should manifest fitness as some function of numerosity.

We can break down the ideas supporting Dawkins' Criterion into one claim about the association of reproductive bottlenecks with complex adaptation and another claim as to the profound importance of selection in generating complex adaptation. When we do so, though, we see that neither claim is fully defensible. Let us start with the idea that a single-cell bottleneck is necessary for complex adaptation, by virtue of being the only way to re-start development. Godfrey-Smith (2009), whilst partially endorsing Dawkins' points, draws attention to cases – such as that of metamorphoses in butterflies and other insects – where development is restarted and a highly distinct new form is arrived at, without the presence of a single-cell bottleneck. No doubt, the presence of such a bottleneck does indeed make the evolution of complex adaptation more *likely*, but this is still only a statistical effect. The presence of a single-cell bottleneck cannot guarantee, nor does the absence of such a bottleneck rule out, complex adaptation. Indeed, the presence or absence of other properties beyond reproduction will also determine whether a system is likely to produce complex adaptation. These include factors like developmental modularity (Klingenberg 2008, Wagner and Alternberg 1996)

As an aside, it is worth noting that, with its dependence on this claim, Dawkins' Criterion is based upon a statistical, rather than deterministic, relationship between the presence of single-cell reproductive bottlenecks and the emergence of complex adaptation. As we have just noted, a reproductive bottleneck in itself will not guarantee complex adaptation, nor will the lack of one prevent the same complex adaptation. This probabilistic character arguably makes Dawkins' Criterion ill-suited to the task of providing the kind of sharp, binary distinction required to absolutely rule out non-reproductive cases of selection and totally avoid our having to employ alternative fitness measures. In his description of "paradigm" cases of natural selection, Godfrey-Smith realises this and employs Dawkins' Criterion as only one element of a cluster concept.

It is useful to have briefly noted that the significance ascribed to the reproductive bottleneck is not uncontroversial. However, this is not the place for a full technical discussion of the issue and, indeed, one is not actually required to reject Dawkins' Criterion. More important here is

the second claim supporting such a criterion - that only instances of selection which can lead to complex adaptation are worthy of our consideration.

By his own reasoning, Dawkins' point is not so much that cases without an appropriate reproductive bottleneck are not selective in character, but rather that they are not *interesting* cases of selection because they cannot lead to novel adaptation. The simple fact, though, is that we are not always concerned with selection as a means to account for or predict the genesis of novel adaptation – making what Godfrey-Smith would call "origin" explanations (2009, discussed here in the previous chapter). Rather, much of the workload of any theory of selection and fitness will be in explaining selection amongst *existing* variation. Biologists are thus very legitimately concerned with population dynamics over relatively short periods of time, due to the differential adaptation in *existing* variants, without the emergence of novel traits. In such cases, Darwinian theory is used to make what Godfrey-Smith calls "distribution" explanations. Thus, we might be perfectly interested in giving a selective explanation of the change in a population resulting from a climate event or, as per our example above, a new pathogen differentially killing off a poorly adapted variant. It would be a very strange version of Darwinian theory that could not be applied to such scenarios. In short, to think that we should only apply Darwinian theory to explain the emergence of complex adaptive traits would be to conflate the research interests of certain individuals or fields with the interests of biology in its totality – which certainly include the explanation of selection amongst existing types.

I see no other obvious ways to support contracting the set of valid cases of natural selection to those which can be captured with a numerosity metric. I also severely doubt that one could be arrived at without running into analogous issues to those faced by Dawkins' Criterion. Thus, any such attempt to rule out considering other metrics will effectively amount to ruling out the validity of certain cases of selection by arbitrary fiat.

3.2. Replace Numerosity With One of These Alternative Metrics

Other authors who have noted similarly problematic examples to those given above have generally sought to replace the standard numerosity metric with some other single metric of their own specification. Thus, Thoday (1953) and Cooper (1984) argue for new metrics based around persistence. Van Valen (1973), whose work is discussed in chapter four, advocates for fitness concepts based upon resource and energy capture in competition.

The idea is that, by adopting a new metric, we will be able to account for all valid cases of selection. This would include both the familiar cases, where the numerosity account functions satisfactorily, as

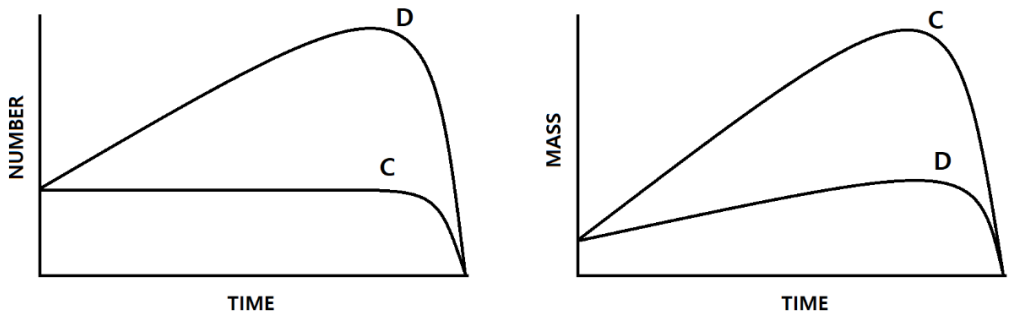
well as those difficult cases which have prompted the new treatment. In order to work, then, the proposed new metric must be able to capture variation in other putative metrics in scenarios where those other metrics explain the action of selection. That is to say, all other metrics which correctly describe subsets of valid cases of natural selection must be able to be reduced to the new metric. We have already seen examples of cases such as the quaking aspen and *Armillaria gallica*, where growth and persistence fail to reduce to numerosity. The question remains as to whether we could hope to reduce all the metrics we have looked at here to some function of either biomass or persistence, such that that quantity could then be used for fitness measurement in all cases of selection.

In reality, none of the metrics we have examined so far are capable of describing *all* scenarios where we might wish to offer a selective explanation. A few examples should suffice to demonstrate that this is the case; with a single example being enough to demonstrate that a persistence-based metric will not be successful in capturing selective changes in either biomass or numerosity.

3.2.1. Numerosity and Biomass Do Not Reduce to Persistence

Let us imagine we have two variants, C and D, of the same species – say of quaking aspen. At the start of our period of observation, the two variants share both the same number of individual groves and the same biomass. Over the same period of time, though, our variants behave rather differently. The groves of variant C grow dramatically in size by sending out the underground runners discussed earlier. C eventually takes up great swathes of land but does so without change in number of groves. Variant D, by contrast, engages in sexual reproduction by seeding, generating a large number of offspring groves, such that D's numerosity increases to many times its starting value. These groves all remain very small, though. The increase in numerosity means that D experiences some growth in biomass, but the small size of groves means it does not approach the sheer size achieved by C. At the end of our period of observation, both groves simultaneously decrease in numerosity and size and become extinct at the same instant.

Thus, we might wish to regard fitness in this case as having been manifested in terms of either somatic growth or numerosity. Whichever of those two quantities we might be interested in, the behaviour of the two variants is quite different, such that we might perceive relative success differently. This is best shown in the graphs below:



However, in this case, any effort to account for what we observe selectively will come to naught if we are equipped only with a persistence-based fitness metric. In terms of persistence, both variants are identical, with this fact blocking any further analysis under a persistence-based monist account of fitness.

3.2.2. Persistence Does Not Reduce to Numerosity or Biomass

There is an extent to which numerosity is inherently related to both persistence and biomass, in that a death will punctuate the end of an existence, but will also reduce a population by one and diminish total biomass by some measure. However, this is not the relationship that would be required for fitness in terms of persistence to be reducible to numerosity or biomass. For this reduction to be feasible, the number or mass (or rate of change of either) of individuals of some type at one point in time would have to be reliably reflective of the subsequent lifespan of that type.

It must be said that this *will* often be the case. In more familiar species, with rough equivalence between individuals in most respects, persistence will be tracked by both numerosity and biomass. Within a standard mammal species, for instance, individuals will have relatively uniform lifespans. Having more such individuals will generally increase the probability of the lineages they belong to still being represented at later points in time. This is the same reason we are happier to predict the continued existence in one hundred years of the superabundant common rat than of the various critically endangered species of rhino and tiger. Similarly, in humans, having a "spare" besides an heir famously helps ensure a family's continued existence. Since individuals within such species will tend to be of roughly similar body sizes - rats and

rhinos will weigh about the same as their conspecifics - biomass will track numerosity and thus will also track persistence. Biomass will also be directly explanatory of persistence for species such as the aspen and *Armillaria gallica*, which will become harder to kill outright as they grow larger and larger.

However, the well-known species of "immortal" jellyfish, such as *Turritopsis dohrnii*, demonstrate both that the lifespans of individuals need not be fixed and that expected persistence need not scale by biomass. Some individuals in such species, when nearing death at the end of their lifecycle, are able to return to their juvenile state and begin their lifecycle afresh, eventually re-growing into adult jellyfish. There is no limit on how many times this regeneration can be accomplished, rendering individuals effectively immortal (Piraino, Boero, Aeschbach and Schmid 1996). Obviously, jellyfish will not be subject to the same kind of open-ended vegetative growth as an aspen or *Armillaria gallica* (we do not observe hundred-ton jellyfish), so their persistence will not be related to somatic size.

Whilst possible, such immortality is not guaranteed and many individual jellyfish will be predated or otherwise traumatically killed – or will simply fail to restart their lifecycle in this fashion and die normally. We also observe variation between closely related species as to whether this regenerative capacity is present (Piraino, Boero, Aeschbach and Schmid 1996). Lifespans in such jellyfish will thus vary enormously, from that of an individual predated in the first days of the first iteration of its life cycle, to individuals potentially persisting for an eternity. For such lifeforms, then, we might wish to offer a longevity-based selective explanation for an individual or type which has persisted for a very long time by means of being well adapted to their environment, even if they have not produced significant numbers of offspring or accumulated new biomass. However, given that these jellyfish are approximately the same size and that we are considering the longevity of individuals rather than lineages, neither a numerosity nor a biomass-based metric will be of any utility to us. Thus, persistence fails to reduce to either numerosity or biomass.

3.2.3. Numerosity Fails to Reduce to Biomass

With cases like the aspen, we observe the possibility that fitness will not be manifested in numbers of individuals. For the aspen, then, I noted that somatic growth was typically more adaptive than reproduction, given the aspen's specific need to rapidly occupy space in the face of competitors. However, Harper (1977:647-650) explains that such strategies will emerge as the result of a trade-off between somatic growth and reproduction, with the possibility that

different strategies might be optimal in different circumstances[6]. Thus, there might well be cases where the adaptive "calculation" differs, such that the risks of prioritising somatic growth, including increased vulnerability to predation and disease, outweigh the benefits, such that reproduction will be prioritised.

Janzen (1977) encourages us to consider the clonal reproduction of aphids and dandelions in just this light. He regards reproduction in both these species as equivalent to the growth of large, singular organisms – but ones taking advantage of the capacities of a spatially distributed entity to resist wholesale destruction by predation, whilst being better able to exploit favoured kinds of resource. In such cases, where increasing in number is more important than growth, we might expect that the total biomass associated with an individual, a lineage or a type would be a poor reflection of its fitness, in just the same way that number was a poor reflection of the fitness of the aspen. In this kind of scenario, we will thus want to offer selective explanations in terms of numerosity, rather than biomass.

Overall, then, it seems that adopting any one metric as an alternative to numerosity will ultimately lead to analogous problems to those already experienced by numerosity-based fitness. Thus, whichever individual metric we adopt, we will lose the ability to explain a certain subset of apparently valid cases of selection. By exchanging metrics, all we do is change which subset of cases this might be, and thus do not really move forward. We can think of this as a general problem of "information loss", such that when we limit our account of fitness to consider only one aspect of population change, we lose the ability to offer selective explanations of change in other aspects. We will return to this theme of information loss in the following chapter.

3.3. Find a Common Currency

I have demonstrated that we cannot reduce the action of selection in terms of numerosity, biomass and persistence to any one of those metrics alone. However, this does not preclude the possibility in principle that there is some *further* metric to which all three could be successfully reduced. Indeed,

[6] Making trade-offs of course suggests that Harper has a kind of "common currency" between reproduction and growth. In fact, Harper conceives of these trade-offs as, in effect, maximising reproductive value (though he does not use that term – Harper refers simply to "numbers of descendants", though cites Fisher in doing so). I have noted here in, section 3.1, that reproductive value will still share the same fundamental problems of numerosity accounts in referring only to number of individuals and failing to fully capture variables like somatic size and persistence. I will return to problems with the reproductive value concept in the next chapter. Despite his discussion thus being couched in a flawed wider framework, though, Harper's description of the biological reality of adaptive trade-offs is still valid and relevant for our purposes here.

when we consider the trio of reproduction, growth and longevity, it is hard not to feel that these are very closely related phenomena and that there must *surely* be some way of capturing all three with one idea.

Whilst I do not propose to ignore this possibility, unfortunately, there are no obvious candidates for such a unifying metric within any of the mainstream literature. As such, I will defer consideration of deriving a common currency for fitness until chapters four and five. There, I will explore what I regard as the most promising routes to such an outcome. However, my investigation across those chapters will show that deriving such a common currency is far from a straightforward task, requiring a fundamental shift in how we think about fitness and selection, whilst still delivering only limited results.

For now, I will set aside the idea of a common currency between the metrics we have been considering. My conclusions in this chapter will thus technically be provisional as to the prospect of deriving a functional unifying metric – though we will discover in later chapters precisely how slim a prospect this is.

3.4. Adopt a Pluralist Position

I noted above that, historically, numerosity has simply been taken *a-priori* to be the single quantity in terms of which selection operates – whilst this was really a non-trivial result in need of theoretical support from the beginning. This initial misconception has been able to be sustained by a long, and now well-reported, fixation on a certain "familiar" subset of the living world, where entities tend to exhibit sufficient intra-specific uniformity in their biologies and life cycles that numerosity would indeed be sufficient to track and explain salient population changes. However, the scope of biological consideration has broadened over time to include more and more disparate cases – such as the examples we have explored above – with significant intra-specific variation in traits such as size and longevity. Thus, we are confronted with a growing set of cases where numerosity is not sufficient to allow for selective explanations to be made. This has revealed that our null hypothesis should really always have been that the complexities of success across the entire biological world will need to be captured in terms of more than one metric.

Really, our theories of fitness have been afflicted by two flawed assumptions; that numerosity is the correct metric to employ and that there is *any* single correct metric to employ at all. Other authors who have sought to replace numerosity with other metrics – Cooper (1984) and Thoday (1953) with persistence-based metrics, for example– have noted that the numerosity approach is dysfunctional and

taken it to be the wrong *single quantity* to capture fitness[7]. However, we have seen the problems of accounting for all of the variation in different quantities which seem relevant to biological success in terms of any one metric. As such, I would make the argument that the *real* source of error is not with specifying numerosity as our privileged metric, but with assuming that we can capture the phenomenon of fitness with *any* single metric at all.

Thus, I propose that we should adopt a pluralist approach to fitness measurement, such that we are willing to make use of multiple different metrics depending upon how biological success is manifested in a particular case, as well as what we are trying to explain and/or predict. This might seem like an alien way to think about fitness. It is certainly a departure from the received view of biological success. However, a pluralist approach to fitness is actually very closely analogous to the manner in which we already happily conceive of success in the human sphere. Hopefully, an appreciation of the parallels to that already-familiar concept will help sanitise my approach here, as well as helping to make my points more intuitive.

Let us take an example. Imagine, for instance, three individuals whom we would think of as having been successful - perhaps the CEO of a sizeable investment bank, a senior cabinet minister in the government and a Nobel Prize-winning academic. Who is most successful? I certainly wouldn't want to say. The banker will likely be a great deal wealthier than the others, whilst the politician will probably be better known publicly and be able to wield the most direct, real-world power. The academic will have made it closer to the pinnacle of their own career ladder than the others and perhaps occupy a more generally respected niche within society, despite their probable lack of widespread personal fame. However, they will be comparatively deficient in terms of real-world power or monetary wealth. If these three meet at a party, it is certainly not clear who should be impressed by the others. Of course, we can say without much controversy that – within relevant career ladders – the cabinet minister has done better than a backbench MP, that the CEO enjoys more success than a junior analyst and that the Nobel Prize recipient is more accomplished than a mediocre PhD student. Across different career ladders, or modes of achievement, human success is thus incommensurable.

This example should be reasonably innocuous, yet contains close analogies to the main features of the account of fitness I propose. Even points where individual readers do not accord with my reasoning in the human case will mirror what I say as regards biological success. Thus, very probably, there will be those who claim that one aspect of human success here is the more important. Some might want to see

[7] To his credit, Bouchard (2008) suggests his new metric as a supplement to the standard approach, thus technically taking a pluralist stance. However, he does provide much detail on how the two measures will interact or on the implications of a pluralist stance for our theory of fitness more broadly.

everything in terms of wealth or material power, for example. However, such claims will inevitably ring hollow in the ears of others. Anyone who wants to claim that one means of success is more important than all the others will seemingly be doing so via pure prescription – ignoring dimensions of achievement seen as important by others. This is equivalent to the problem of information loss we face when attempting to prioritise any one fitness metric to the exclusion of all else.

My position regarding fitness measurement is fairly straightforward. At least until such time that we can derive some common currency to make the different aspects of fitness commensurable, we should be permissive in allowing for biologists to make use of whichever metrics are required to capture the action of selection in a specific case and according to their specific explanatory aims. Thus, we might explain selection amongst, say, familiar mammals in terms of number, but might switch to describe the selection of *Armillaria gallica* in terms of biomass or persistence. Indeed, as we have seen with aspen, it is possible that we might be able to coherently describe the same scenarios in terms of different metrics simultaneously – effectively "changing frame of reference" by offering selective explanations of the same system in terms of changes in different quantities. As per the tripartite distinction I set out earlier, the question as to the most appropriate measurement scheme to deploy such metrics within will still be subject to debate, as it is currently. Even if we want to think about fitness in terms of biomass, for instance, we can still debate whether to do so as a retrospective "realised" quantity or as a propensity. It is important to note that, just as for the human concept of success, we do not need to give up a singular idea of fitness in order to recognise that fitness is a multi-dimensional phenomenon, with different aspects which might not be commensurable to one another. This general idea of fitness as a multi-faceted phenomenon is not a new one, and is already very ably described by Thoday (1953) in his paper "Components of Fitness".

4. Implications of a Pluralist Account

Crucially, then, a metric-pluralist approach to fitness has the positive outcome of allowing us to expand the explanatory scope of our theory of natural selection to be able to account for selection in terms of quantities other than number of entities – and to do so without sacrificing any current explanatory capacity. Moreover, I have argued that, in this case, we should not see the transition away from a monist account in order to do so as a retrograde step. Rather, the standing assumption that fitness should, or even could, be expressed in terms of a single metric was always an unjustified one.

Beyond this payoff, though, there are some other important implications emerging from the move to a metric-pluralist account. I will examine a few of the more salient amongst these.

4.1. Fitness Ranking

One apparent "problem" with metric pluralism is that we will not always be able to directly compare the fitness values of entities within a Darwinian population, meaning that we will not necessarily be able to generate rankings of individuals according to their fitness. In short, this means that we will not always be able to definitively say which of two individuals or types within a Darwinian population is the fitter. This is because it is possible that different individuals within the same Darwinian population might display different levels of success in more than one dimension of fitness simultaneously. In such a case, we would have no objective way of stating which individual or type is absolutely fittest overall.

For example, we might encounter two strains of some species, one which exclusively exhibits success in terms of reproduction, the other exclusively in terms of somatic growth - perhaps one aspen which has lost the ability to produce seeds and one which has lost the ability to form runners. In such cases, we can measure the fitness of the reproductive variant in terms of number and that of the expansive variant in terms of biomass. However, we do not have a common currency by which to render these values commensurable, so we cannot say in absolute terms whether a 50% increase in biomass of a single aspen grove represents a greater or lesser degree of biological success than producing 10 small new offspring groves[8]. Matters will be even more complex if we introduce simultaneous differences in persistence as well. The general problem is equivalent to that of deciding whether our banker or our politician above were the more successful – the quantities which we are comparing are simply incommensurable.

Of course, I must be clear that it will definitely still be possible to make absolute comparisons of fitness between individuals or types which realise their fitness at least predominantly in terms of only one quantity. In short, we will still be able to compare like with like. Thus, we can rank fitness values within "familiar" species, from cattle to mice to fruit flies to many kinds of bacteria, where biological success is meaningfully exhibited in terms of number of offspring only. Similarly, we will be able to compare aspen to one another in terms of biomass and *Turritopsis dohrnii* in terms of their longevity. Such comparisons are the equivalent of being able to rank human success within a specific career ladder – by saying an academic is more successful than a PhD student, or a cabinet minister than a backbencher. In reality then, given evolutionary biology's historical focus on life forms whose fitness is realised in the convenient terms of numerosity, we will still be able to make the vast majority of absolute fitness comparisons we do currently. Indeed, we will only really add to this ability, with the possibility of

[8] There would be a temptation here to simply compare somatic size and reproduction in terms of raw biomass, but this will likely fail to represent the comparative adaptive worth of these two different manifestations of fitness. As has been discussed in section 3.2.3, offspring might be more or less adaptively "useful" than their equivalent mass in new somatic tissue.

comparison between the members of species who demonstrate biological success in terms of other quantities.

4.2. Is Pluralism a Less Desirable Form of Theory?

Whilst some readers will be well-disposed to pluralist accounts generally, others will inevitably regard the transition from a monist to a pluralist stance as a retreat from robust theory – part of a general trend of too-readily resorting to pluralism in the face of theoretical difficulty. I have provided a rationale against the idea that monism should actually be our default position as regards fitness. However, I also share the ambition to account for fitness in terms of a single quantity – and generally to capture the natural world with maximally parsimonious theories. Thus, I have recommended a pluralist account here as no workable common currency is available *as yet*. Even just the quantities we have discussed here have failed to reduce to one another, let alone other potential metrics. In chapters four and five, I will explore the possibility of deriving such a common currency in the form of a new, unifying fitness metric. It is not impossible in principle that such a metric should be derived in future, but pluralism serves as a theoretical "backstop" until such time.

With all this said, if we could arrive at a common currency between different fitness metrics, there would likely remain cases where we were interested in the particular means by which fitness was expressed, and thus where measurements of multiple quantities would still be useful. To take an analogous example from the human realm, we might be able to compare the cash reserves held in different currencies by two organisations in absolute terms by converting the value of each into Pounds Sterling. However, it would still be a matter of genuine interest and significance as to which specific currencies those reserves were held in; whether circumstances were such that they had favoured US Dollars or Japanese Yen, for example. Even if the organisations' positions were currently equivalent, their particular currency choice might be particularly important in predicting how they fared in response to future market changes.

In just the same way, it might be biologically salient as to which particular aspects of fitness are relevant in specific cases of selection. For example, even if we could absolutely weigh fitness achieved in terms of growth and reproduction, it is still revealing to note that the aspen will tend to favour the former because of the ability to rapidly occupy space being particularly advantageous in its specific circumstances (Bouchard 2008). Indeed, even within current practice, applying a standard, numerosity framework of fitness, Endler (1986) records the habit of working biologists to make use of various different specific fitness measurements according to convenience and explanatory interest; this being in spite of a presumable theoretical commitment to fitness as some single function of number or

offspring production. We have good reason to believe, then, that pluralist measurement will survive the derivation of a common currency between fitness metrics in the case that this proved possible.

4.3. Directions for Useful Application

Many attempts to extend selective explanation, both to non-standard levels of organisation in the biological world and to non-biological substrates, have run afoul of problems with identifying reproduction, replication or a suitable analogue in the domain to which selection theory is to be applied (Lewens 2018). Recognising the action of selection in terms other than numerosity seem likely to greatly facilitate such extensions. The space available, and reluctance to over-extend tangents, mean that I will make only a few brief remarks here as to how metric pluralist ideas could be usefully applied to problems in other areas. Despite my brevity, though, this does indeed represent a significant positive in adopting a pluralist stance.

Debate around clade selection is an area where the standard assumption that fitness is a business of counting has been particularly detrimental to progress. Okasha (2003) rules out the possibility of clade selection on definitional grounds, due to reproduction not being present at the level of clades. However, the ability to perceive selection in terms of growth and persistence greatly improve the prospects of extending selective explanation to clades. The same should be true for other non-standard levels of selection.

There have been similar problems in assigning fitness values in other areas. Notably, within the literature on cultural evolution, there has been significant discussion as to the extent to which the spread of "memes" or "cultural replicators" (where even the terminology used implies commitment to a numerosity approach) can be suitably analogised to reproduction or replication (Lewens 2018). Thus, there might well be significant potential for development in cultural evolutionary theory by relaxing the notion that selection must operate only in terms of numbers of offspring, copies or similar.

4.4. Questions Raised

I have explained that a pluralist approach to fitness is worth adopting by virtue of its allowing for a substantial increase in scope for selective explanations, with no significant downsides. However, it must be acknowledged that a pluralist approach does raise some questions of its own. Specifically, if we are to allow more than one valid fitness metric, we might wonder how we decide if some new putative metric is a valid one or not. That is to say, we might ask how we should bound the set of valid fitness metrics.

Given what I have said above as to the fact that the standard numerosity approach should really have been accompanied by a principled justification for focussing exclusively on that particular metric, I would hold that standard monist accounts similarly lack criteria defining valid fitness metrics. It would perhaps be better to say, then, that a pluralist approach simply makes this issue more *apparent*. How one perceives this issue will vary according to one's existing theoretical commitments, though, and is not worth further discussion.

Those happy with a pluralist approach might be content to say that all of this is simply relative to the explanatory interests of the biologist. A valid fitness metric would just be one that can be coherently applied to make explanations for a case of selection in which a biologist is interested. However, making metric validity relative to explanatory interest only really pushes the question back one level of analysis, so that we might instead enquire as to what set of qualities makes a certain scenario the proper candidate for selective explanation in the first instance. Presumably, our theory cannot allow us to assess absolutely *any* physical system via absolutely *any* fitness metric, so long as the mood takes us, and expect the results to be meaningful and informative. At some level, real boundaries need to be placed on a pluralist treatment so that the evaluations it makes can have meaning at all.

In practice, of course, biologists are eminently sensible and the idea that they will engage in wholly vacuous explanatory endeavours is largely a hypothetical one. However, the fundamental issue underlying these questions is a broader one. More generally, a metric pluralist stance gives us cause to consider our overarching fitness concept - which is ultimately required to guide our measurements and accord them meaning. I have already noted, by analogy to our concept of human success and to other accounts of fitness, that there is no reason why we cannot hold an idea of fitness as a multi-dimensional, but nonetheless conceptually singular, phenomenon. However, this only outlines the shape of the relevant fitness concept rather than giving much indication as to its contents.

My stated purpose in this chapter was to discuss only fitness metrics. As such, I will reserve discussion of these broader issues for chapters four and five. There, I will explore the possibility of uniting the metrics here at a conceptual level, analysing how those aspects of biological success relate to one another and what might distinguish valid from invalid metrics. At the same time, I will also return to the idea, from section 4.3 here, of deriving a common currency fitness metric. These issues are closely related, but separable – I will eventually find a way to conceptually unite the different metrics that does not offer a workable common currency between them.

Conclusion

This chapter has challenged the assumption that fitness must always be denominated in terms of some number of entities. After setting in place terminology that will be useful throughout subsequent chapters, I discussed examples where fitness appears to be manifested in terms of somatic growth and/or persistence. A systematic assessment of possible responses to these examples showed that neither sticking to a numerosity metric nor switching to a similar monist account based on either persistence or biomass was tenable. As such, I recommended taking a pluralist stance, allowing different measures to be applied even to the same case of selection.

Importantly, a pluralist account allows us to extend selective explanation to previously problematic cases. However, I noted that it does notionally also mean that we will not always be able to generate absolute fitness rankings. I argued that this is unlikely to be a problem where selection concerns "familiar" species, meaning that most current fitness comparison would still be valid. Any such issues can also be balanced against the prospects of making significant progress in extending selective explanation to non-standard levels of biological organisation and non-biological substrates; such as clade selection and cultural evolution.

Finally, I noted some questions raised by a move from monism to pluralism as regards our broader understanding of the phenomenon of fitness. I will return to these issues in chapters four and five. In the meantime, in the next chapter, I will continue my analysis of the most fundamental assumptions underlying standard treatments of fitness with an examination of the role of time in fitness. This will extend arguments analogous to those made here into the temporal dimension, with broadly similar conclusions being reached.

III

FITNESS AND TIME

As noted at the beginning of the previous chapter, fitness is often conceived in terms of success in some competition to contribute offspring (or tokens of some gene or trait type) to the next generation. We have now taken to task both the idea that selection is inherently competitive and that success under selection is captured only by counting numbers of entities. Now, we move on to the assumption that the relevant time frame to assess fitness is of the order of a single generation.

This is a feature of "conventional" accounts of fitness that has been challenged rather more often in the existing literature. Indeed, I will differentiate two classes of problem relating to how fitness measurements function over time which have been discussed. Here, I will focus on the specific set of issues whereby short-term measures of fitness and longer-term success appear to be in tension. Much of my discussion will concur with and augment the reasoning in papers by Beatty and Finsen (1989) and Sober (2001). I will arrive at a pluralist position regarding fitness measurement over time, along the way rejecting the utility of generating "overall" fitness rankings in many cases. The argument there will echo that in the previous chapter. Finally, I will set out how taking the form of pluralism I advocate to its fullest extent allows us to understand how levels of biological success at different points in time constrain one another and can be subject to selection.

Schematically, then, my argument in this chapter will be organised as follows:

1. The Naïve View

To begin, I give a brief explanation of what I characterise as the "naïve" view as to fitness and time. I note that a single-generation time frame captures fitness perfectly well in many cases. The act of ranking individuals or types in terms of fitness seems natural in these instances and serves as a reliable guide to the expected occurrence of competitive exclusion where zero-sum competition drives selection.

2. Where the Naïve View Breaks Down

I note the extensive literature around fitness and time dealing with questions of how best to derive the mathematical expectation associated with fitness under the propensity account – or

whether it is coherent to do so at all. However, I clarify that my own focus here will be the more fundamental, but less frequently addressed, question as to the interaction between short and long-term biological success.

I discuss a couple of widely cited examples where a naïve view fails in this manner. In considering why these cases are problematic, we arrive at the question of what we require from an account of fitness in the first instance. Precisely what we want from an account of fitness will vary according to our wider understanding of selection. However, I consider that a basic requirement spanning most treatments is that fitness measurements ought to be useful in the explanation and/or prediction of evolutionary change/population dynamics. I also note an apparently related, common desire to rank entities according to their relative fitnesses.

3. Responses to Problem Cases

I follow Beatty and Finsen (1989) and Sober (2001) in rejecting long-term definitions of fitness, along with attempts to privilege measurement at *any* single point in time. The main issue for these responses is a problem of information loss, analogous to that in the previous chapter, whereby the explanatory potential of our account of fitness is severely limited. I add a discussion of the possibility of measuring fitness as a summation of reproductive output over time, but find this to be subject to the same fundamental problem. This analysis leads naturally to what I label "intra-case" pluralism regarding fitness measurement over time.

4. Implications, Competition and Maximisation

I note that this kind of intra-case pluralism will make it impossible to provide "absolute" or "all-time" fitness rankings of entities in all cases of selection. However, I question the utility and validity of such rankings. I argue that the desire to habitually rank entities under selection is linked to a mistaken conception of natural selection as universally competitive. I also argue that maximisation accounts of fitness fail to justify a monist approach to fitness measurement over time.

5. Example - Fluctuating Selection

To illustrate my points, I consider an example of fluctuating selection, presenting a case where neither ranking the entities involved, nor making any singular measure of their fitnesses, will be useful in explaining the complex population dynamics observed.

6. Joining the Dots

I show that the intra-case pluralist approach balances losing the ability to rank variants by facilitating discussion and explanation as to how the level of success manifested at different points in time depend upon one another. I illustrate with an example based on the evolution of the cicada's lifecycle.

I conclude by noting the parallels between my arguments in this chapter and the last. In both, a problem of information loss prompts a broadly pluralist position. As such, this chapter can be considered as extending the same general approach to fitness into the temporal dimension.

Despite these parallels, the points in this chapter are largely separable from those in the last. For simplicity's sake, then, I will stick to working with a standard numerosity metric throughout almost all the discussion here, referring to fitness simply in terms of reproductive success.

1. The Naïve View

It is common to think of fitness in terms of single-generation reproductive success. Of course, we might prefer to conceive of selection as operating at the level of traits or genes rather than that of individuals – and relatedly might like to work in terms of inclusive fitness. More generally, then, we might state our starting "naïve" view as the idea that fitness values will be some function of the contribution of an individual, type or genotype to the population or gene pool of the next generation. Whatever the nuances though, what is salient here is that the naïve view considers fitness as relative to biological success over a *single* generation – that is, over the shortest of time frames.

This naïve view does indeed function perfectly well in very many scenarios. Imagine, for example, examining a population of Kettlewell's (1955) famous peppered moths in the kind of polluted industrial setting where the melanic variant thrives. The higher single-generation reproductive success of the darker variant in the prevailing conditions seems to very straightforwardly capture its higher fitness relative to the paler variant. The relevant fitness values calculated will help us to predict and/or explain the success of the melanic type over time, whereby the numbers of dark peppered moths relative to light steadily increases over multiple generations. Indeed, if the two varieties are in competition, the higher fitness of the melanic type would potentially allow us to predict and/or explain its eventually driving the pale type to extinction. In this straightforward kind of case, success now will be predictive of success later. Accordingly, rankings are robust and useful. Here, the dark type is clearly fitter across any time

period in that specific, sooty environment and this ranking is predictive of its long-term success versus the pale type.

The single-generation approach also has some appeal at the conceptual level. We like to think of selection generally as a "selfish", "short-sighted" process, rewarding only short-term advantage. This accords with the popular view, as per Brandon (1990:24–5, also quoted in Sober 2001) that selection ''proceeds through generational time'' and thus ''has no foresight".

Nevertheless, I label this starting approach to fitness as "naïve" intentionally, in light of the fact that it has long been known to throw up problems in certain scenarios where selection does not proceed so straightforwardly as for our peppered moths above. In these scenarios, a single-generation approach to fitness seems to misrepresent the action of selection. As a result, we are left wondering how we might alter our approach to fitness in order to accommodate these cases.

2. Where the Naïve View Breaks Down

It has long been realised that there are cases where this naïve view ceases to function satisfactorily. Though they are often dealt with in the same papers, we can separate the problems for the naïve view into two separate groupings. One deals with mathematical problems in deriving a satisfactory expectation of reproductive success within the propensity account of fitness associated with Mills and Beatty (1979). I will briefly take note of this issue. However, this will largely be for the purposes of disambiguation with the second problem, concerning irregularities in the relationship between short and long-term reproductive success. My own focus in this chapter will be on this second problem.

2.1. Mathematical Expectations of Reproductive Success Fail to Track Actual Success

Under a propensity account of fitness, it has been repeatedly shown that details concerning stochastic variation in reproductive output, both within and between generations, can cause trouble for the typical method of calculating the expected reproductive success associated with fitness. Specifically, that is the method using a simple, arithmetic mean to calculate expected reproductive output from the relevant probability distribution of reproductive outcomes (as per Mills and Beatty 1979).

The most well-known and widely cited result here is Gillespie's (1977) original demonstration that two types with the same expected reproductive output (calculated via an arithmetic mean) might produce very different numbers of offspring over multiple generations where those two types exhibit different variances in the numbers of offspring they produce. Despite sharing the same "expected" reproductive

output, then, we would generally anticipate the type with lower variance in their offspring number to become significantly more numerous over time – with the magnitude of this disparity between the types' success growing with generation number. Similar results have also been demonstrated where there are differences between the skew of the relevant probability distributions and where there is stochastic variation in offspring production not just within generations, but between them (Beatty and Finsen 1989, Sober 2001, Rosenberg and Bouchard 2015, Krimbas 2004)

Various mathematical fixes have been suggested, with issues addressed by switching to a geometric, rather than arithmetic, mean in certain cases (Beatty and Finsen 1989:27, Crow and Kimura 1970). However, no consensus has been reached, either on a potential solution or if a complete remedy will be possible at all (as per Krimbas 2004). Indeed, in Beatty and Finsen's own paper on the issue, even those advocates for the propensity account admit they do not have a conclusive solution.

The immediate reason to mention this body of literature is to clearly differentiate a closely related, but ultimately separable, area of study from the specific question I wish to address here.

2.2. Disparities Between Short and Long-Term Fitness

In the same papers where Beatty and Finsen (1989) and Sober (2001) deal with the issues above, those same authors also discuss problems where short-term fitness and long-term biological success do not accord with one another, such that the naïve view seemingly fails to capture biological success over time as we might hope. To clarify, we will take a couple of commonly cited examples where this tension between short and long-term fitness becomes apparent.

2.2.1. Example - Maintenance of Sex Ratio

The problem of how precisely the regular 50:50 sex ratio observed across familiar sexually reproducing species is selected for was noted by Darwin himself and remained mysterious for decades. The best-known solution was provided by Fisher in his *Genetical Theory of Natural Selection* (1930)[9].

Under a naïve, single-generation view of fitness, the biological success of individuals is considered simply in terms of how many offspring they contribute to the next generation – with these offspring counted equally to one another. In the case of sex ratio, this means that a naïve view would consider offspring of either sex to contribute equally to the fitness of their parents. Those producing four male offspring would be just as fit as those producing four females, two

[9] Though his argument seems to have been derived from the work of others, including that of J.A. Cobb (Edwards 1998).

males and two females or any combination adding up to the same total number. This seems to make sense in context of selection as a short-sighted, selfish phenomenon, acting only to reward short-term reproductive success.

Assigning equal fitness here will also correspond to our likely intuition that the sexes of a species ought to be attributed the same "overall fitness". Certainly, we would not typically regard one sex as "fitter" than the other generally, as both are necessarily required for offspring production and we could hardly imagine one sex outcompeting the other and driving it to extinction.

Thus, from this naïve perspective, it really is not clear why the relative frequencies of the sexes in any given population should not drift well away from the 50:50 ratio we so typically observe. There would simply be no selective "reason" for individuals to produce any particular ratio of offspring types. Fisher's explanation was that the subsequent reproductive success of male and female offspring in the next (grand-offspring) generation will not be equal. He expressed this insight by ascribing differing "reproductive values" to offspring of different sexes (we revisit ideas of "reproductive value" in section 3.2).

In modern terms, Fisher effectively explained that sex ratio is maintained by negative frequency-dependent selection. Thus, where a population has a surplus of male offspring, competition to mate with relatively scarce females will leave the average male less likely to secure matings – and thus produce offspring – than the average female. In these circumstances, then, where two individuals produced the same number of offspring, but one produced all-male and the other all-female offspring, the two individuals might exhibit the same immediate reproductive success – and thus the same naïve, single-generation fitness – but the individual with female offspring would end up with a greater number of grand-offspring than the individual producing males.

Thus, where we have a population starting with a surplus of one sex, over multiple generations, the sex ratio will be re-adjusted towards an equilibrium point where the members of both sexes enjoy the same level of reproductive success. In modern terms, we would call this an "evolutionarily stable strategy" (or ESS). Overall, then, selection can be thought of as providing a reward to those individuals with a heightened tendency to produce whichever sex is scarce. Crucially, though, this reward is deferred to the grand-offspring generation, rather than being granted in the immediate, offspring generation.

Since we do generally observe stable 50:50 sex ratios, we have an indication that selection is operating here in terms of this extended time frame and not in line with the single-generation, naïve view of fitness. Indeed, we can perhaps take the decades of confusion as to how sex ratio was maintained as testament to the capacity of that naïve approach to fitness measurement to mislead us as to the action of selection and stand in the way of our ability to explain. It is also interesting that the explanation of how sex ratio is maintained requires us to consider differential success between the sexes – going against our normal intuition that the "overall" fitnesses of the sexes should be equal.

2.2.2. Example – Avian Clutch Size

The go-to example of the potential disconnect between short and long-term fitness is the observations of reproductive restraint in avian egg-laying associated with Lack. A couple of decades after Fisher's discussion of sex ratio, Lack (1947, 1948) produced the work which has become perhaps the most well-known instance of de-linkage between immediate fitness and longer-term reproductive success. Lack's and other biologists' empirical work on avian clutch sizes demonstrated bird species apparently laying fewer eggs than they were capable of producing. Under a naïve, single-generation approach to fitness, we would expect selection to have favoured the evolution of birds laying as many eggs as possible and would accordingly have ranked the most immediately reproductively successful as the most fit. The idea of reproductive restraint, then, ostensibly seems highly "un-Darwinian". However, Lack noted that, when birds had an increased number of offspring, they tended to have fewer grand-offspring. By contrast, birds showing reproductive restraint and laying smaller clutches, tended to have more grand-offspring.

Lack's explanation was that young hatching into smaller broods were individually better provisioned than those emerging from larger clutches, to the extent that the former were significantly more likely to fledge successfully and ultimately to reproduce (Sober 2001 usefully discusses this example in terms of viability and fecundity as components of fitness). Thus, lower fitness in the immediate, offspring generation seems to – almost paradoxically (as per Beatty and Finsen 1989) – produce greater reproductive success in the grand-offspring generation. Once again, then, we have what could be thought of as a deferred reproductive "reward" in the grand offspring generation and, again, selection appears to be acting in favour of reproductive success over a longer time frame than is captured by a naïve, single-generation approach to fitness. Thus, if an investigator was only to examine immediate-term reproduction, they would rank individuals with larger clutches to be fitter and make poor predictions as to the future population dynamics.

2.3. The Fundamental Problem

In both cases here, short-term fitness fails to capture the action of selection in the same way it does for more straightforward scenarios. Thus, in such instances, short-term fitness is a poor tool to directly explain or predict long-term biological success. Short-term fitness here also fails to accurately rank the entities involved in selection according to our impressions of their "overall" biological success over time. Thus, whilst short-term measurements might instruct us that Lack's more fecund layers are fitter than reserved types, this runs strongly counter to our clear impression that the more reserved layers are fitter "overall". As alluded to above, Beatty and Finsen note (1989:20) that, in cases like that of Lack's birds, the particular causal relationship between short and long-term fitness means we have the apparently perverse possibility of explaining low long-term success in terms of high short-term fitness.

What arguably makes these problems more interesting than the mathematical concerns over expectations described earlier is that the issue of short versus long-term fitness generalises outside the propensity account. Indeed, papers on the issue (such as Thoday 1953, 1958) historically long-predate the development of any explicit propensity approach. In spite of being more widely applicable and having been recognised for a much longer period of time, though, this problem has been discussed less than those concerns specifically regarding expectations of success.

2.4. What Do We Want From Fitness?

Of course, levelling the criticism that the naïve view somehow fails in these examples begs the question as to the precise standards to which we are holding our fitness measurements. In short, what do we actually want from a fitness measurement? It might be easy just to spot that *something* is wrong with the naïve view, but it is important to be explicit about our requirements before we consider how we should then respond to the problems we have observed. We will need to know how to properly assess any prospective new approaches to measuring fitness over time.

What *precisely* we want from our treatment of fitness will depend to a large extent upon the wider theory of natural selection it is embedded within. There is room for considerable variation, especially at the conceptual level. For example, some (such as Brandon 1990) will want to regard fitness as representative of adaptation, whereas others will strongly reject this idea (such as Krimbas 1984, 2004).

However, there are some fundamentals which it seems almost everyone will want from their fitness measurements, regardless of how those measurements are then interpreted within a wider conceptual scheme. In particular, we are very likely to want our fitness measurements to be of some practical use to investigators in making explanations or predictions of biological success. After all, without some payoff in terms of explanation and/or prediction, it is not clear why we should bother to measure fitness

at all. This desire has been reflected in the response to the examples above, where I note that a naïve, single-generation treatment does not allow us to explain and/or predict success over time.

As a minimum, then, I take it that we should be pursuing an approach to measuring fitness over time that facilitates explanation and prediction more satisfactorily than the naïve view. For the above examples, this will mean doing a better job of allowing us to explain why more prolific layers do not prosper over multiple generations and why sex ratio does not simply drift over time.

I am not alone in making this kind of basic requirement from an account of fitness. In their treatment of these issues around fitness and time, Beatty and Finsen (1989:19) set out their own "minimal requirement", stating that "however 'fitness' is defined, it must at least be positively correlated with actual evolutionary success, i.e., with persistence or increase in frequency" so that it can "sustain the role nominally played by fitness in evolutionary explanation".

Somewhat relatedly, fitness often seems to be associated with the ability to rank individuals in terms of their overall biological success. Thus, we might think that an optimal treatment of fitness will mean that we are able to say that X is fitter than Y and Y is fitter than Z overall. Ranking and explanation are typically taken to go hand in hand. Above, then, we might think that if only our fitness measurement had registered that the more reserved layers were the fitter *overall*, then this fact would allow us to explain their subsequent success as compared to the more fecund type.

I will attend to the idea that an improved treatment of fitness over time should do a better job of generating plausible rankings than the naïve view in cases such as those above. However, I find that ranking is often separable from, and largely irrelevant to, the business of explanation and/or prediction. When this de-linkage occurs, I argue that we should favour explanatory/predictive capacity over the generation of fitness rankings. I hold, as per similar remarks in chapter one, that our desire to habitually rank the participants in selection is a hangover from the mistaken idea that selection is an inherently zero-sum competitive phenomenon.

3. Responses to Problem Cases

Multiple responses to these problem cases are possible. If we wish to retain a monist account of fitness measurement over time, qualitatively similar to the naïve view, we can either move to a longer-term measure, assessing fitness at a later single point in time, or take some kind of summation of reproductive success over an entire time window. I follow Beatty and Finsen's (1989) and Sober's (2001) exposition

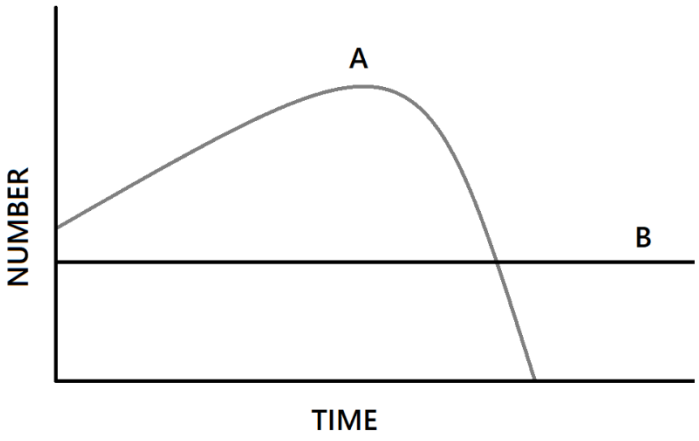
and rejection of the former option and provide my own points against the latter. This brings us to the better option of adopting a pluralist approach.

3.1. Longer-Term Measures

It might seem that the obvious response to the problem cases we have looked at is simply to consider fitness as manifested over a longer period of time. Certainly, for Lack's more reserved layers, a longer-term view seems to make a better job of explaining our observations.

Within the literature, Thoday (1953) and Cooper (1984) develop approaches that seek to measure fitness in terms of much longer time frames. Thoday argues that we should equate fitness with the probability of persisting 10^8 years into the future. Such ultra-long-term views of fitness will effectively become measures of the persistence of a lineage or type. Thus, Cooper presents his own account of fitness in terms of Expected Time to Extinction (ETE) – the anticipated time until the relevant lineage dies out.

Sober follows Beatty and Finsen in considering these long-term approaches to fitness via a graph of the form shown below[10]:



This graph depicts a scenario akin to Lack's clutch size example, in that the initially more-fecund type, A, is less successful over the longer run. In the case depicted, though, A then goes to extinction, whereas B maintains steady numbers until the end of the observed time period. Looking at this kind of number/time graph, our initial intuition might well be that assessing fitness over a longer time frame is

[10] I have retained the overall form of this graph, though have changed some minor details – irrelevant to my points here – in terms of labelling and presentation, simply for it to sit better alongside my other figures.

the most sensible course of action. This would rank B as fitter than A, whilst then helping to explain A's extinction and B's relative long-term reproductive success.

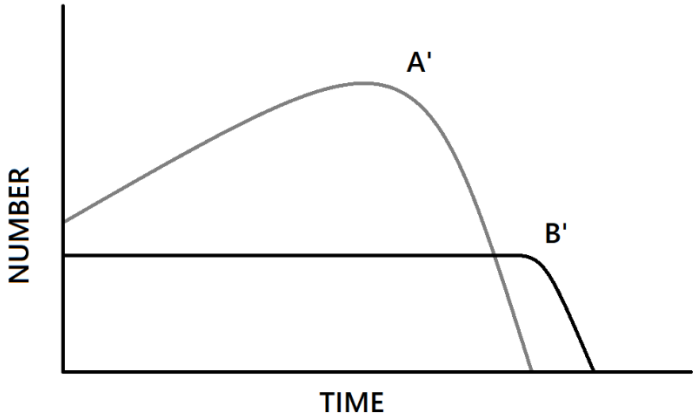
So far, so good. However, Beatty and Finsen (1989:21) and Sober (2001:29) point out that we are taking a rather narrow view of the questions we might wish to ask about what we observe. Thus, as I put it, we might not only be interested in making judgements about "overall" performance, but might be just as interested in making selective explanations as to specific details of population dynamics. Different investigators will have different concerns and it is perfectly reasonable that a biologist might be interested in giving an account as to why A was so initially successful. In doing so, it seems natural that they may wish to offer selective explanations – and thus invoke a shorter-term idea of fitness.

If we are willing to consider only long-term fitness, though, we lose the ability to make these kinds of short-term selective explanations. As such, by moving to a longer-term view, we might be able to rank types so as to better capture their respective "overall" success in our eyes, but we emerge with an impoverished ability to make some legitimate selective explanations, which would have been valid under a short-term view.

Indeed, this will be the case for whichever point in time we decide is the "correct" one to measure fitness. We will always have legitimate interests in offering selective explanations for population dynamics over the whole time period we observe. Measuring fitness exclusively in terms of any one time frame will necessarily put some subset of these explanations out of our reach.

Thus, we arrive at a problem of information loss analogous to the one encountered in the last chapter (where we were only considering fitness measurement in an "instantaneous" sense). The number/time graphs here encode more biologically salient information than can ever be captured by a single, unidimensional fitness value. Any attempt to choose such a *single* value will simply mean choosing *which* subset of information to lose and thus which set of selective explanations we will be unable to make. Certainly, this seems like a high price to pay if we are doing so simply in order to make better fitness rankings.

To help make this point more clearly, I would add the following slight variation of Beatty and Finsen and Sober's initial graph:



Here, we maintain much the same scenario, but with the change that B' also goes to extinction shortly after A'. So, which type is fitter? Readers might find that their intuitions are less certain here, as the two types look rather more closely matched in terms of "overall" fitness. B' does persist a little longer than A', but not by much, and it looks like A' was more reproductively successful for much of the observed time period.

Previously, we might have been prepared to accept a long-term approach to fitness on grounds that it was clear that B was fitter than A overall and that we should be prepared to make some explanatory sacrifice in order to be able to make "correct" rankings. Here, it is much less clear that one variant is fitter than the other *at all*. Indeed, which is fitter is arguably not particularly interesting as compared to explaining the specifics of the population dynamics we observe.

Regardless, then, of any uncertain or changing intuitions as to which type is fittest "overall", we will still have a legitimate interest in making selective explanations as to specific aspects of the observed population dynamics. Thus, regardless of whether or how we decide which of A' or B' is fitter "overall", we can still very reasonably wish to make the same selective explanation alluded to above as to just how A' enjoyed such rapid reproductive success in the short term. Whilst this would presumably employ a short-term fitness measure, we might also wish to take a longer-term view to explain why B' was the more persistent. One of these will accord with whatever our personal intuitions are regarding the "overall" fitness of A' and B' – but one will not, and privileging one measure might meet our explanatory needs, but go against our intuitions about ranking.

This idea of ranking and explanation/prediction being something we have to trade off against the ability to rank in terms of fitness is a theme we will return to in section four. In the meantime, though, this modified scenario with A' and B' brings us to the next possible solution in dealing with cases where short and long-term fitness de-link in the observed manner.

3.2. Summed Reproductive Output Over Time

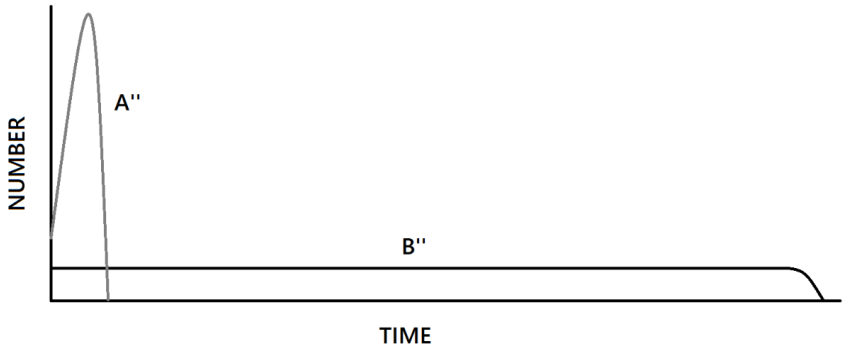
Some readers will already find themselves asking, when looking at my second graph above and considering whether A' or B' should be considered fitter, "well, which had most offspring overall?". After all, it seems plausible to say that Lack's reserved layers restrict their brood sizes in the short term in order to maximise their overall reproduction across multiple generations.

Whilst neither Beatty and Finsen nor Sober's papers consider this potential solution to the problem of fitness measurement over time, the idea of summing reproductive success right across the time period being examined seems sufficiently plausible to merit analysis. Indeed, aspects of the more technical biology literature effectively move in this direction to deal with concerns over fitness and time. Fisher's explanation of stable sex ratios implemented the idea of "reproductive value" – making an analogy to the methods by which assets are valued in finance, where a single current monetary worth is ascribed to a recurring cash flow over all time. These ideas are still current, and Grafen (2006) has more recently developed Fisher's ideas on reproductive value in greater detail so as to merge them with his Formal Darwinism project.

We can regard this kind of measure as making something like a summation of reproductive output over multiple generations. Indeed, this kind of "summation" approach will perform well in many cases. Clearly, the idea of reproductive value was already useful in explaining the maintenance of sex ratio and it would allow us to rank Lack's layers in a way that corresponded to their long-term success.

However, we cannot escape the previous problem of information loss. This issue becomes even more pronounced in cases with more complex population dynamics – as per my example in section five. However, even in the simplest cases, summation potentially loses a great deal of biologically salient information by, in graphical terms, simply taking the areas under the number/time curves we have been looking at, with no regard to those curves' specific forms.

To clarify, I would add a further iteration of our basic number/time graph:



Here, we see that A'' is hugely more reproductively successful in the short term, but then rapidly goes to extinction. B'' maintains steady, but much lower, numbers and goes to extinction only at a much later time. Once again, then, it seems fairly clear that we should regard B'' as the fitter type overall – the population of A'' appears to simply have "burnt itself out" via excessive fecundity.

Let us say that the areas under the curves for A'' and B'' are equal, thus ranking A" and B" as equally fit by summed reproductive output. Regardless, a biologist might still be very interested in explaining the specific population dynamics we observe – accounting for the differences in the particular form of reproductive success of A'' and B'' over time, even if the total is the same.

Indeed, a summation measure will not always correspond to our intuitions on ranking. Here, it looks very much that B'' was the fitter variant "overall" and that A'', as noted, has "burnt itself out" early on. However, it might even be that the area under the curve for A'' is greater than B'', such that A'' produced more total offspring over the same time period. This would be feasible if, for example, A'' had produced large numbers of less-robust offspring, who were unsuccessful in resource competition and were soon driven to extinction. A'' would be defined as fitter, very much against our intuitive judgement.

The insight that our intuitions as to "overall" fitness over time appear to vary in the dimensions of both reproductive success and persistence bolsters our findings in the previous chapter as to the multi-dimensional nature of fitness. Here, though, it is sufficient to establish that summation measures place inherent limits on our ability to explain interesting biological phenomena.

Remarks on ranking help cast doubt on the worth of summation, but are based largely on intuition and so are less meaningful. Regardless of how we decide to rank the "overall" success of these types,

though, we will still want to explain the specifics of the dynamics we observe. Doing so will necessitate a treatment of fitness that encodes *all* of the relevant information. No single, unidimensional measure, however formulated – whether a certain point in time, summation of reproductive output or otherwise – will be capable of capturing all this information. This leads us to our next putative solution.

3.3. Pluralism

If we reject the possibility that any single measure – whether at a single point in time or a single "summation" measure across time – will provide for all the selective explanations and/or predictions we might wish to make, then we inevitably end up embracing some shade of pluralism. Thus, Beatty and Finsen's and Sober's analyses, as well as my additions, all clearly point towards a pluralist approach to fitness measurement over time as the only way to avoid the general problem of information loss curtailing our capacity for explanation and/or prediction.

Different modes of pluralism are possible. Thus, we might adopt what I will refer to as an "inter-case" pluralist position, whereby we accept the possibility of alternating the specific measurement we apply between different cases of selection. Thus, we might adopt a longer-term measurement of fitness in cases such as Lack on clutch size, but retain a shorter-term measure in a case such as our peppered moths from earlier, where this is appropriate for our purposes.

Crucially, though, we would still only apply one kind of measurement for each specific case. There would be one "correct" measurement for every scenario, supposed to capture the action of selection as it manifests there. However, from our analysis so far, it is clear that inter-case pluralism will not be sufficient. Applying any one measure to the more complex cases of selection that necessitated this analysis in the first instance might help in generating plausible fitness rankings, but will inevitably lead to the same problem of information loss curtailing explanatory capacity. For Lack on clutch size, a longer time frame fitness measurement would let us rank the restrained layers as fitter "overall", but is not a great deal of use in explaining the initial population dynamics where those restrained layers fall behind in the short term. Thus, inter-case pluralism does not leave us much further forward than the naïve view.

A more permissive form of pluralism is what I will refer to as "intra-case" pluralism. This would allow us to measure fitness within multiple time frames for the same case of selection. In this version of pluralism, we can apply different measures of fitness as required to explain all aspects of the population dynamics we observe, according to our explanatory and/or predictive interests. Thus, we might apply short-term fitness measures to explain the initial reproductive success of A above, but make use of a longer-term view in explaining the persistence of B.

Now, whilst clarifying the idea of intra-case pluralism, it is worth explicitly noting that, whilst it has been convenient thus far to discuss "short" and "long" term time frames for fitness measurement, we are not only discussing two possible ways of measuring. This usage has really just been to simplify discussion, as well as reflecting the fact that the relatively simple cases we have considered thus far divide fairly neatly into two sequential phases of behaviour. As we will see in section five, more complex instances of selection might call for measurements of fitness to be made at an indefinite number of points in time, in order to explain intricate population dynamics. As such, intra-case pluralism will not simply be a matter of potentially applying both one long-term and one short-term fitness measurement, but an indefinite number of measurements across the full range of available time frames.

4. Implications, Competition and Maximisation

For some readers, it might have seemed obvious that we should immediately switch to tracking fitness at all points in time, as allowed under the intra-case pluralist approach I set out. However, it was important to show why it was *necessary* to adopt this position because it is accompanied by some substantial trade-offs versus the naïve view. In particular, this pluralist view will not always allow us to rank the "overall" fitness of entities under selection together – which might seem counterintuitive. However, I hold that our desire to habitually rank participants in selection is simply a residue of the mistaken idea that all selection is competitive. I also note that, even if some maximisation account of fitness were brought forward guaranteeing our ability to generate "overall" fitness rankings, this would not be sufficient to warrant a return to a monist approach.

4.1. Loss of Ranking

As noted, inter-case pluralism would have allowed us to retain overall fitness rankings in all cases. If we apply only a long-term fitness measurement to Lack's birds, we are able to rank the restrained layers as the fitter type. However, moving to an intra-case pluralist position, this changes. Such an account, by its very nature, means there will not necessarily be a single "correct" fitness value to ascribe to each entity.

Of course, there will be cases where one type simply outperforms another in all dimensions simultaneously. With our peppered moths above, if the melanic type is more reproductively successful in all generations and eventually persists beyond the pale type, then we are clearly justified in claiming that the darker variant is fitter overall.

However, other cases will not be so clear cut. We can refer to the case of A' and B' above – where B' persists a little longer, but A' appears to have been significantly more reproductively successful over very nearly the same duration of time. In this case, my proposed response would be simply to discard the prospect of ranking the A' and B' and focus on the mechanics of predicting and/or explaining the particular form of their population dynamics over time. In such cases, we might like to say that one entity is fitter than another *within a certain time frame*, but not "overall". This might seem perverse, but I believe that it is our constant desire to rank entities under selection that is, in fact, at fault here. This deserves some discussion before I illustrate the de-linkage between ranking and explanation via a further example in section five.

4.2. Rejecting Ranking

As noted in section 2.4, the ability to rank individuals according to their "overall" biological success might be thought of as a goal for our treatment of fitness over time. Thus, losing this ability might be seen as a problem for the account I suggest. However, I believe that the desire always to rank the participants in selection is a hangover from the idea that natural selection is inherently competitive (countered in chapter one) and, more specifically, that competitive exclusion will always be in operation. Ranking might be predictive/explanatory where such conditions do indeed hold. Under resource competition, for example, the fitter type will prosper at the expense of other variants and would typically be expected to drive those other types to extinction.

However, the fact is that these conditions will not be universal and that, where they do not hold, ranking participants will often be a particularly unhelpful way to understand the action of selection. In chapter one, I defined the category of "parametric selection", containing many paradigm instances of selection that proceed without any competition at all; and thus certainly without the action of competitive exclusion. Parametric selection might be at the hands of adverse weather conditions, soil or water pH, ocean currents or any number of other non-competitive, environmental factors. In such cases, survival and/or success will not be a matter of competition against peers, but simply a matter of "clearing the bar" set by the environment. Competitive exclusion would not be predicted and types might co-exist indefinitely (as in our recurring example of Lewontin's Bacteria).

When the biological success of one type has no necessary impact on other types, it is unclear what we gain by the act of ranking in itself. As we have seen already, and as I will set out again in section five, ranking can be meaningless or even detrimental to the business of explanation/prediction.

4.3. Maximisation

A more plausible way to defend ranking is via a "maximisation" account of fitness, which conceives of selection as reliably maximising one particular measure in all cases. Numerous different maximisation accounts of fitness have been put forward, with Birch (2016) providing an excellent overview. Indeed, Birch notes that "maximisation" has meant several different things to different authors, only some of which might actually be relevant to our concerns here. Thus, some maximisation accounts might only expect fitness to trend upwards under selection, whilst others will expect selection to eventually bring fitness to an optimal value. Accounts will also vary as to whether they take maximisation to be occurring at the level of the population's mean fitness or at the level of the individual maximising its own fitness.

All forms of maximisation account have proved controversial, though – most notably because all accounts thus far proposed have notable exceptions, where observed reality does not maximise fitness in the manner they suggest. Thus, Birch notes that no existing mainstream maximisation accounts function universally, but only apply within tightly bounded conditions. Grafen's (1999, 2014) Formal Darwinism project is perhaps the best known and best developed contemporary maximisation account, but so far fails to capture fundamental factors like mutation and frequency-dependent selection – the latter of which has been particularly interesting to us here already (in Fisher's explanation of sex ratio, for instance) and which we return to in section five.

However, the work of Grafen and others is ongoing. Let us say, then, that some maximisation account was brought forward with direct impact on the issues in this chapter, such that it was demonstrated conclusively that selection universally acts to maximise fitness over one particular time frame. Perhaps we were to find that some function of total reproductive output over all time is always selected for, for example.

This might lead us to make a few inferences. First, we would be justified in ascribing priority to the time frame over which fitness was maximised. We could indeed warrant this as the "most important" time frame to consider when looking at an instance of selection. In turn, then, this would allow us to give objective fitness rankings in all cases. Ranking according to a measure which selection will always maximise would indeed capture the "overall" fitness of types.

We might then also be tempted to discard all other measurements of fitness over other time frames on apparent grounds that our maximisation account tells us what actually matters about the scenario we are examining, with everything else being extraneous detail. However, this is not justified. Even though we might be warranted in prioritising one measure and can thus provide absolute overall fitness rankings as described, this does not mean that we will not have legitimate explanatory interests in accounting for

the specifics of population dynamics over time which might not be captured by that single maximised measure. As we saw in our examples of A and B above, even if we regard one type as fitter overall, with greater long-term reproductive success, this does not preclude our wishing to offer a selective explanation for the short-term success of another type.

In short, then, a maximisation account prioritising one measure of fitness over time, and thus facilitating overall fitness rankings in all cases, will still not allow us to escape the same problem of information loss discussed in section three. Indeed, the irrelevance of overall fitness ranking to the explanation of complex population dynamics was already discussed in section three and will be clearly shown in the example of fluctuating selection in section five.

4.4. Explanation and Prediction

As we have seen above, and as I will demonstrate once more in the example of fluctuating selection that follows, trying to explain or predict the specifics of complex population dynamics armed with a simple idea that one type is "better" than the other will be a fool's errand. For our purposes here, insistence on the capacity to generate rankings as we seek to work out how we ought to approach fitness measurement over time will mean we keep returning to the same problem of information loss we have discussed above – simply exchanging which subset of explanations we lose out on as we switch one approach for another. Fundamentally, the desire to rank impels us toward singular, unidimensional measures of fitness, as these allow us to then straightforwardly order the values we generate. However, no single value can encode the full potential complexity of population dynamics over time.

Thus, I hold that fitness and selective explanation need not have anything much to do with "overall" rankings at all. Indeed, I will now consider a more complex case of selection, where overall ranking is largely irrelevant to explanation. There, we will not perceive observed population dynamics as being the result of one type being fitter than the other, but still find a great deal of interesting activity which we would reasonably want to subject to selective explanation via appropriate fitness measures.

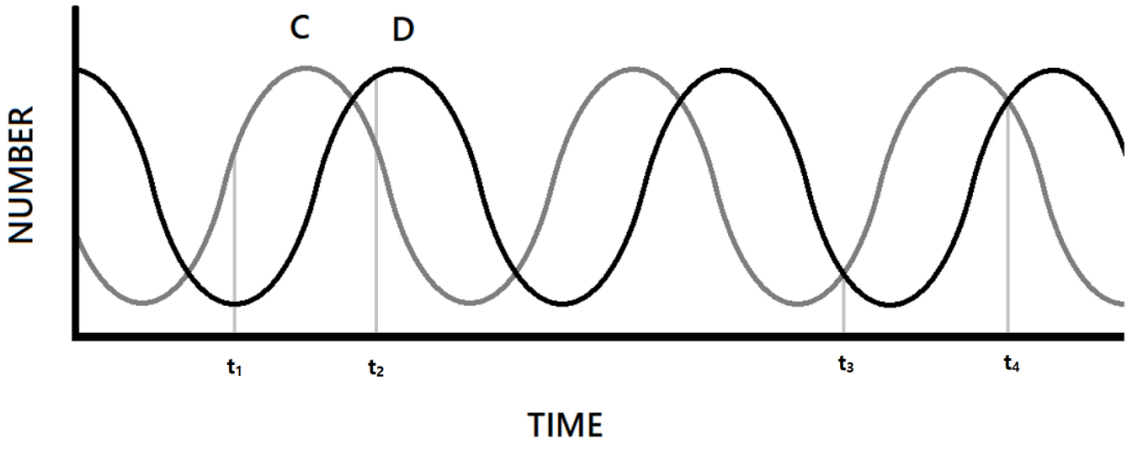
5. Example - Fluctuating Selection

An example of fluctuating selection will illustrate my points so far. Fluctuating selection comes in a few forms and can have different underlying drivers. Often, fluctuating selection is a result simply of regular fluctuation in environmental conditions, such that different types will be successful at different times (as per Wright and Dobzhansky 1946 and Wittman et al 2017).

Often, though, fluctuating selection will be driven, at least partially, by zero-sum competitive interactions between types (as in Tabiana and Abderrahman 2019, where mate competition drives fluctuating selection). Fluctuating selection has been particularly interesting to biologists as it allows the maintenance of polymorphisms in a population (Brisson 2018) without competitive exclusion, despite zero-sum competition being in force. Thus, fluctuating selection can allow for multiple competing types to persist over an indefinite period of time with zero-sum competition, without one driving the others to extinction.

Fluctuating selection is often driven by negative frequency-dependent selection – that is, the same form of selection responsible for maintaining sex ratio, discussed above, with its characteristic de-linkage between short and long-term success. One oft-discussed form of negative frequency-dependent fluctuating selection is that associated with Tinbergen's (1960) predator search image hypothesis. Here, frequency-dependent selection drives fluctuation, as predators "learn" the appearance of, and thus disproportionately predate, the most common types in a population. This means increased survival and reproductive success for less common types, at least until their numbers climb to become most common – causing that type to become subject to heightened predation and thus for their numbers to rapid decline. An excellent example is fluctuating selection in the predation of the polymorphic snail *Cepaea nemoralis* by thrushes (Cain and Sheppard 1953). This process, whereby predation constantly switches to the most common type, is thought to have maintained snail shell polymorphisms since at least the Pleistocene (Owen 1966, Ayala and Campbell 1974).

Fluctuating selection will typically result in the characteristic "boom and bust" population dynamics shown in generic form in the following graph:



This graph may be recognised by readers familiar with the predator/prey cycle. The largely analogous dynamics show that phenomenon as effectively the inter-species manifestation of the same fundamental mechanism discussed here in the intra-species case.

Presented with the above graph, we obviously perceive complex and interesting population dynamics. By the same token, though, singular, unidimensional, "macro-level" assessments do not indicate a particularly interesting scenario. The dynamic equilibrium between the two types suggests that we should rank both as equally fit. Certainly, there is no move towards competitive exclusion/extinction of either type at the hands of the other.

A summation measure of fitness will also simply consider the two types equally fit, as the total reproductive output associated with each (the area under each curve in our graph) will tend to identical values over long runs of fluctuation. However, we will still want to explain these complex dynamics. Indeed, as an example from the literature, we see repeated attempts at explanation of very similar dynamics in the various analyses of the Hudson Bay Company's 200-year fur trapping records (MacLulich 1937) documenting alternating fluctuation in lynx (predator) and hare (prey) populations. Elton and Nicholson (1942), for example, attributed the fluctuations to changes in climate before Gilpin (1973) later fitted the observations to the now-familiar predator/prey model.

Summation and any other single "overall" measure of fitness return us to the problem of information loss – discussed at length above, but shown more starkly in this case – where so much information and potential explanation is given up. Taking any single measure of fitness at *any* one particular point in time will be just as problematic. For Lack's birds, or in Beatty and Finsen's and Sober's scenario of A and B, discussed previously, one can coherently argue that a longer-term fitness measure is the single "correct" one. This will not be the case here, though.

For instance, measuring fitness at t_1 will rank C as much fitter than D, whilst making a similar measurement later in time, at t_2, will give us the opposite impression as to ranking, with D coming out much fitter than C. Crucially, whichever single measure we made would not be helpful in predicting the state of the population at t_3 or t_4.

The only way to capture and explain all the population change over time observed here is by making multiple measures of reproductive success at different times. Thus, we arrive at the intra-case pluralist approach discussed above. This allows us to explain whichever aspects of the relevant population dynamics we might be interested in. Should we need to, we can happily apply different measures to

capture the reproductive behaviour at t_1, t_2, t_3 and t_4 as we see fit. This comes at the expense of being able to rank types, but – as explained – I do not see this as a serious loss.

Indeed, we already observe something of a pluralist approach to fitness, particularly in cases of fluctuating and/or frequency-dependent selection, within the empirical biology literature. Thus, we see work considering the variety of fitness measures that might be required in such circumstances (for example Saether and Engen 2015, see also Siepielski et al 2010 and Orr 2010). In the same vein, it was concerns around frequency-dependent, and especially frequency-dependent fluctuating selection, which led Kojima to state in his clearly titled paper "Is there a constant fitness value for a given genotype? No!":

> It is my personal view that no serious and capable investigator has believed the values of genotype fitness to be constant in an absolute sense. (Kojima 1971)

Overall, then, fluctuating selection provides us with an especially clear example where we require assessments of biological success at multiple instances of time in order to capture, and thus explain/predict, the action of selection over time. What is more, this is a case where the relative "ranking" or any "overall" measure of the fitness of the entities involved is largely irrelevant – or potentially even detrimental – to this business of explanation/prediction.

6. Joining the Dots

Transitioning from the naïve view, then, we have lost the ability necessarily to assign a single value to, and thus crucially to rank, an entity's fitness over time. As per our examples above, this means there will be cases where we cannot objectively state which of two types is the fitter over time. Ultimately, this is part of giving up on a view of selection as inherently competitive – always having winners and losers – that we showed to be false in chapter one. All we can do in certain cases is to chart and explain biological success over time and say that one type is fitter than another only at one particular instant. We can describe and explain what we see but must refrain from necessarily declaring victors.

However, the intra-case pluralist approach to fitness measurement over time also confers some positive payoff. As we have seen, particularly in our example in section five, considering fitness at different times allows us to satisfactorily explain complex population dynamics in cases where fixating simply on which variant was the fittest overall would obscure biologically important detail.

Taking this approach to its limits, we can also start to "join the dots" and consider how success at one point in time depends upon, and can be explanatory of, success at other points in time and how these relationships can be subject to selection. Thus, we can explain instances where immediate success comes at the expense of longer-term fitness. This is in line with Beatty and Finsen, who comment on the interdependence of success in different time frames. For scenarios where long-term success de-links from short-term fitness:

> …inasmuch as high short-term fitness causally underlies low long-term fitness (and hence low long-term success) in such cases, reference to high short-term fitness constitutes a deeper explanation of the phenomenon than reference to long-term fitness (Beatty and Finsen 1989:20)

Perhaps most interesting, we can also start to consider how selection can favour restraint in success at one time by allowing for the realisation of inflated success in a later period, along with the constraints governing the viability of such strategies. This is the kind of "trade-off" or "investment" of short versus long-term success we have already observed in simple form in Lack's birds. A great deal could be written on the detail of the potentially complex interdependences between fitness manifested at different points in time. For our purposes, though, an example based around the life cycle of the cicada will serve to demonstrate how intra-case pluralism confers significant explanatory and/or predictive gains in a more involved scenario, where later outcomes are constrained by the earlier states a population must move through en route to those outcomes.

6.1. Example – The Cicada

When we consider cases like Lack's birds, where short-term "sacrifice", "restraint" or "investment" leads to longer-term "reward", there will typically be a limit in practice on precisely how much short-term reproductive success can be traded off in this manner, whilst allowing the strategy as a whole to remain viable. One advantage of this intra-case pluralist approach, then, is in allowing us to more clearly grasp the constraints on these kinds of trade-off.

To illustrate this capacity, we will look at an idealised model, based on a real-world example. I will consider a single-generation case, simply to set out the relevant mechanisms and considerations as clearly as possible. However, the same reasoning can apply just as readily to multi-generation cases, as I will note later.

Thus, I will consider a case based on the suggested route for the evolution of the cicada. There are many species of cicada displaying broadly similar biologies and – particularly relevant here – life cycles. Cicadas reproduce above ground as a winged insect but spend the vast majority of their life cycle living

underground in the form of a pre-reproductive "nymph", feeding on fluids from tree roots. The cicada only emerges above ground for a brief period at the end of its life to mate (Williams 1995).

The time spent as a subterranean nymph can vary both within and between species, ranging from one right up to 17 years. What are referred to as "annual" cicadas can actually spend up to nine years underground. However, individuals in such species spend different durations as nymphs, so there will always be some cicadas from such species emerging to reproduce each year. More well-known are the "periodical" cicadas. These species synchronise their life cycles so that all remain underground for the same duration, before emerging to reproduce all at once. Lloyd and Dybas (1966a, 1966b) suggest this strategy means that the above-ground predators of the cicadas will be deprived of food for a prolonged period and that, when the cicadas do emerge en masse, rather than piecemeal, they will do so in sufficient numbers to swamp the now-reduced predator population they encounter. Krebs and Davies (1993:125) describe this as an “evolutionary race” between predators and prey as each extend their lifespans. Specific periodic cicada species will remain in the nymph stage for either 13 or 17 years, though the exact duration will be the same for all members of a specific species.

Let us consider periodical cicadas, so that the life cycles of all members of the population will be in sync. Thus, we begin with a population of nymphs, below ground, waiting to emerge and reproduce. Whilst underground, these juvenile cicadas cannot be accessed by the predators which prey upon their above-ground, reproductive form. Where these predators are dependent upon eating cicadas for a sufficiently large proportion of their diet, then, the predator population will be depleted the longer the cicadas remain underground. As such, when the cicadas do emerge to reproduce, they will encounter a lesser degree of predation hindering their efforts. This will correspond to achieving increased reproductive success, making for a greater total population of new nymphs at the end of the reproductive phase.

We might think, then, that our cicadas should remain in subterranean safety almost indefinitely – or at least until the above-ground predator population has gone extinct. We might thus predict that nymphs will remain below ground for the full duration until all above-ground predators have starved to death or left the area – say 20 years – before emerging to reproduce unhindered.

This is already an interesting conclusion when we consider the possibility that other varieties might have reproduced many times, cycling through several generations, in the same time frame. Whilst the payoff after one generation will be higher for such "restrained" variants they will have postponed that payoff by some time. As such, we might think of cicadas remaining underground for several years,

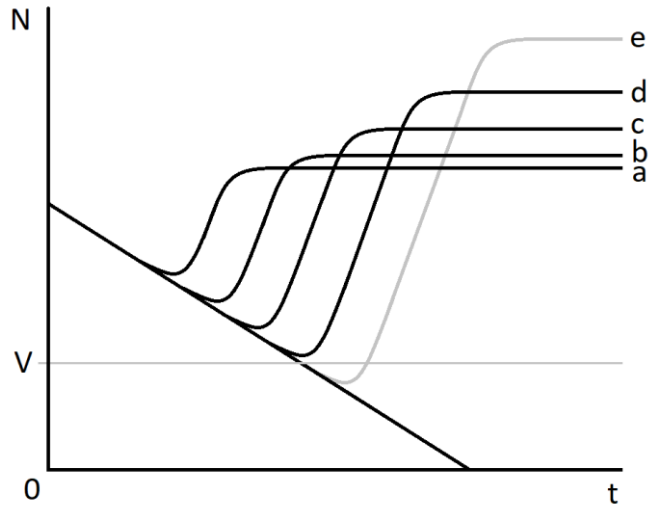
rather than just one or two, as comparable to Lack's birds in showing short-term reproductive restraint in service of a longer-term reward.

However, we should add an additional layer of detail by noting that there are other ways for our cicadas to die than at the claws of their above-ground predators. There will be an attrition rate during the period where the cicadas are underground and this will ultimately limit the duration of the sub-terranean element of their life cycle. Other predator species – either living underground or digging for food – might prey upon nymphs. The trees the nymphs feed on might be killed, starving the juvenile cicadas. Otherwise, deaths might be caused by pathogens or by general misadventure – perhaps due to excavations by larger animals digging burrows or humans conducting building work.

Say that the summed effect of these underground deaths is a reliable, linear decay of the nymph population with time spent in the subterranean phase. Since nymphs cannot reproduce to replace such losses, if they remain underground for too long, the cicadas will go extinct – and this might happen before they have waited out the total extinction of their above-ground predators (which we will assume to be the case here).

Indeed, even before the population goes to zero, there will likely be a critical level such that, if the population dips below a certain number, it becomes unsustainable and will inevitably go to extinction. Here, I will name this critical value the "viability" level (N=v) of a population. We might think of this as an "event horizon" for extinction such that, once reached, the population cannot recover and extinction is unavoidable. This additional idea of a viability level does not add much to this particular case beyond considering extinction (N=0) in itself. However, as I will note below, in other cases there are likely to be additional limits on viable populations not so immediately related to extinction. Thus, it seems worthwhile to begin with a boundary for population change beyond the trivial N=0.

Now, this possibility of the subterranean mortality rate pushing the nymph population below its viability level places an upper bound on the duration the nymphs can spend below ground. Below, we see a number/time graph showing the different outcomes for our cicada population remaining in the nymph stage for different periods of time:



The final curve ***e***, shown in grey and corresponding to a subterranean nymph-stage of 16 years, is the notional result of allowing the predator population to fall to even lower levels than represented by the previous curves. However, this is not a tenable strategy in practice, as it would mean taking the nymph population below its viability level, so that extinction, rather than increased reproductive yield, would result. Overall, we would expect a population adopting the optimal strategy represented by curve ***d***, corresponding to 15 years underground, to outperform populations adopting other strategies, as these will face either a higher-than-necessary level of above-ground predation (curves ***a***, ***b*** and ***c***) or see subterranean deaths drive the population to extinction (***e***).

Observing such a population in real life, then, our explanation for the lifecycles we observe will ultimately need to refer to the specific form of population dynamics over time – in effect, to the entirety of the number/time curve above – rather than to any solitary measure. Even if we are only interested in the strategy maximising total offspring production, to understand how this is determined, we will have to understand the way in which success at different points in time are interdependent and the various constraints on population dynamics.

The same fundamental phenomenon might be realised in different ways. Thus, just as our cicadas must remain above a certain critical numerosity at all times, there might be other organisms where achieving *too great* a numerosity at any given time might be equally deleterious as – for example – demand for food or other resources might outstrip supply, resulting in deaths (similar to the reason for Lack's birds' laying restraint). We could imagine this also being a problem for our Cicadas, such that $\boldsymbol{d}$ is, in fact, too high a number of offspring to avoid damaging resource competition, and so $\boldsymbol{c}$ evolves as an optimal trade-off between time underground and sustainable resource use above. We now have the idea of a specific envelope constraining viable strategies for realised success over time. More complex effects should also be possible, but will not be explored here.

Critical readers will realise that this cicada example concerns a strategy realised over a single generation (even if the absolute generation time might be highly variable). As noted, considering our cicadas in absolute time, we observe reproductive restraint in aid of later payoff akin to that shown by Lack's birds. However, if we insist on measuring time as a function of generation number, we can indeed account for this case as an instance of selection favouring maximal single-generation reproductive output.

I would caution that the idea of regarding one-year and 17-year generations (as per real-world cicada generation times) as fully analogous seems highly artificial. However, this argument is not worth getting into. The specific model I have set out here was chosen to simplify discussion. The same general causal structure – where a period of restrained reproduction allows for a later period of increased reproductive output, with constraints on viable strategies– can be manifested in many cases, including those spanning multiple generations; where the relevant strategies will evolve much like single-generation life histories.

As such, we should be able to find plentiful cases where single-generation immediate reproductive success is sacrificed in aid of reproductive output multiple generations hence, where our approach to fitness helps us explain how this is possible. Lack provides a simple example here. However, in a more complex case, we might observe social insects spending several generations prioritising the construction of a large nest for their colony, subsequently yielding a deferred reward in terms of increased reproductive capacity. We would be able to note that any decrease in reproductive rate during the construction will have tracked above the level where the population would have gone to extinction and that, had it not been possible to sustain the population whilst building the colony, the behaviour could not have been selected for.

The point of this discussion has been to demonstrate how considering fitness at multiple points in time facilitates consideration of how levels of success at different points in time are interdependent and how trade-offs between short and long-term reproductive success are constrained. To understand these

phenomena, we will often have to examine the full "trajectory" of success over time. The resulting logic here is closely analogous to that employed when considering the probability that a population managing to evolve from a locally optimal phenotype to a globally optimally one via sub-optimal intermediary stages. In such a case, the extended metaphor of the adaptive landscape is invaluable and we readily move to discussion of whether it is feasible that the population will be able to traverse the adaptive valley between its own current peak and the higher one which it might climb.

In order to work out whether such a move might be possible, both the depth and width of the valley in question are relevant, as we must ascertain how much immediate fitness will be sacrificed and for how many generations. Thus, we are accustomed to the idea that the specific shape of the path between local and global optima are already acknowledged to be relevant to explanation or prediction as to whether certain evolutionary changes are feasible. This is very similar reasoning to our evaluation with our cicadas as to whether the population dynamics required for a certain trade-off between short and long-term fitness are feasible without resulting in extinction.

A great deal more could be said on these strategies trading off success at different points in time, especially in analogy to work on adaptive landscapes. However, what has been said here should be sufficient to demonstrate the increase in explanatory power we gain in moving away from the naïve view and towards the intra-case pluralist position I have set out.

Conclusion

I began by noting instances where what I characterised as a "naïve" approach to measuring fitness within a single-generation time frame, breaks down in the face of more complex cases of selection. Of the two broad problems facing the treatment of fitness over time, I opted to focus here on cases where the short and long-term success of entities seem to be in tension with one another.

Considering possible solutions to this issue, I largely concurred with and extended the arguments of Beatty and Finsen (1989) and Sober (2001). As such, I noted that any approach continuing to assign a single, unidimensional value to fitness over time will inherently mean losing the ability to explain biologically salient population dynamics.

Shadowing the logical progression of the previous chapter, I put forward an "intra-case pluralist" treatment of fitness measurement over time as the only way to avoid this problem of information loss. I noted that this approach means giving up on the ability always to rank entities according to their "overall" fitness over time – which might have been considered a goal of an account of fitness over

time. However, I challenged both the usefulness and validity of ranking entities in this manner. Generally, I hold that our desire to rank the entities under selection together is left over from the erroneous idea that selection is inherently competitive.

Balancing this loss, I demonstrated that our intra-case pluralist approach confers a significant increase in explanatory power by allowing us to readily consider how levels of fitness at different points in time depend upon one another, the constraints on these relationships and how they might be selected. Thus, we move from interplay between short and long-term success being problematic for our account of fitness, to a more developed treatment actually facilitating our understanding and explaining the most complex instances of such interdependence.

IV

FITNESS AS CONSUMPTION

In chapter two, I suggested that fitness ought to be conceived of as a multi-dimensional phenomenon, with multiple valid metrics which are incommensurable with one another. Similar ideas appeared in chapter three. As such, I have argued for a close analogy between fitness as a measure of "success" in selection and the concept of "success" in the human world, insofar as both are conceptualised as singular despite being manifested in multiple, apparently incommensurable ways.

However, in chapter two I also stated that my conclusion regarding metric pluralism was provisional on the possibility of some “common currency” metric being found to render somatic size, persistence, numerosity and any other valid metrics commensurable. One was not available in the mainstream literature, but this did not preclude its existence. Relatedly, I also noted that allowing multiple valid fitness metrics left us with conceptual-level questions around what valid fitness metrics have in common and how these can be distinguished from invalid alternatives.

Across this chapter and the next, then, I will explore these related issues of potential unification at the level of metric and concept. Here, I will begin by looking at a segment of the literature which, whilst far from the mainstream, promises to unify our various aspects of fitness with a single metric. Thus, I will examine the idea of measuring fitness as some function of the capture and/or consumption of essential resources or raw energy. In effect, this approach offers the ability to reconcile disparate “outputs” associated with fitness (growth, reproduction etc) via the “input” of resources or raw energy by which they are achieved. Whilst I find it to be fundamentally unworkable, I note that this approach does have some promising aspects, which provide a starting point for my own account developed in chapter five.

Schematically, the current chapter will be structured as follows:

1. Foundations

I specify the problem we are dealing with more precisely and explain why an approach to fitness focusing on the consumption of energy or resources offers an attractive route to pursue the

unification of different fitness metrics. I also include a brief note on methodology, relevant across both this and the subsequent chapter.

2. Van Valen's Accounts of Fitness

Van Valen's work is introduced as the premier example of an existing, consumption-based approach to fitness. Analysis of his work will serve as a proxy by which to assess the merits of similar "consumption" accounts more generally. I note the development in Van Valen's thinking and thus partition his work on fitness into two iterations, labelled his "basic" and "advanced" accounts. These are explained separately, with additional comment on the role of competition in Van Valen's advanced account.

3. Problems for Van Valen and Similar Accounts

I discuss problems for Van Valen's approach. Multiple criticisms are possible, but I focus on a subset likely to generalise to any similar approach to fitness based around resource or energy consumption. Thus, the problems around competition, efficiency and non-metabolic entities I identify serve to rule out "consumption" approaches to fitness in general.

4. Where Next?

Despite dismissing the work of Van Valen and anything like it, I argue there was much that seemed promising about this approach. As such, I propose making a similar attempt at deriving a common currency for fitness by viewing the natural world at the level of the underlying physics, but by shifting back towards examining the "output" of entities under selection, rather than the "input" represented by their consumption of resources or energy. This should offer a more direct way of rendering the different aspects of fitness commensurable, without recourse to faulty ideas about competition, covering non-metabolic entities and being less vulnerable to "efficiency" concerns that emerge with attempts to measure output via input.

My concluding remarks lead into my attempt to derive a thermodynamic account of fitness in the next chapter.

1. Foundations

Closing chapter two, I noted that this pluralist image of fitness poses a number of questions. If multiple fitness metrics are possible, what then determines whether a possible metric is a valid one or not? How do we explain, for instance, that the number, biomass or persistence of the entities we are interested in

might reasonably measure their fitness, but not other facts about those entities, such as their total surface area or colour? This might seem like an odd question, but answering it will also help us explain what exactly the different metrics we have examined have *in common* with one another. Ultimately, this can allow us to characterise the fundamental phenomenon of fitness – to flesh out our fitness "concept" in my parlance – providing an explanation as to why we have so far not been able to reduce the metrics we have examined to a single "common currency".

The conclusion that fitness is a multi-dimensional phenomenon in the manner described was reached after demonstrating the impossibility of completely reducing the various proposed fitness metrics to any one of their number. Any attempt to do so was shown to result in the loss of information that might be relevant to forming legitimate selective explanations. For instance, dealing with fitness entirely in terms of numerosity might lose information on differences in somatic size or persistence, which a biologist might like to account for in terms of selection. Indeed, I noted that, even if it were possible to derive a single metric, which reduced all the genuinely salient information to one single quantity, it is likely that investigators would still be interested in distinguishing between different aspects of fitness – such as growth and reproduction – in their explanations.

Despite all this, though, it can seem deeply counter-intuitive that reduction to a single fitness metric should not be possible. When we look at the various metrics that have come up in our analysis, they all seem to be closely related – that is, it appears very much that entities conducting activities like growth, reproduction and prolonging their persistence are all engaged in the same fundamental business. Indeed, the concepts already blur into one another in the existing literature. We have already noted how reproduction and growth can be difficult to distinguish, even in empirical observation (with the stock example of the quaking aspen). I will also explain how theoreticians have gained insight from blurring the conceptual boundaries between those two phenomena. As set out in chapter two, ideas of survival and persistence have a long pedigree in evolutionary theory and it is common amongst both theoreticians (such as Williams 1970) and laypersons to regard the reproduction measured by typical numerosity accounts of fitness as ultimately serving the perpetuation of lineages (though we saw in chapter two that persistence resists reduction to numerosity).

Thus, we arrive at the means to salvage a single fitness metric, which was mentioned, but not explored, in chapter two. This is to reduce all the current metrics to some *further* quantity, which is capable of capturing all the salient aspects of those metrics' variation in one single measure, without losing any important information. The strong similarity between the metrics we have looked at makes this appear to be a promising avenue, and readers might wonder why I have not explored this option previously. However, it is not at all obvious what this kind of metric, or its conceptual underpinning, would look

like, with no examples forthcoming in the mainstream literature. A sufficiently detailed discussion would have derailed my previous analysis in chapter two, so was deferred until this chapter and the next.

1.1. Fitness as "Consumption"

In this chapter, I will examine an approach to fitness that does offer a common currency between existing fitness metrics and which does have a presence in the literature – but which is nonetheless very far from the mainstream. I will refer to instantiations of this general approach as "consumption" accounts of fitness.

Consumption accounts approach fitness from the basic insight that all of the activities we associate with fitness – phenomena like growth and reproduction – are united in being inherently costly in terms of material resources and/or raw energy. Thus, ostensibly, we have good reason to expect that resource and/or energy use will track fitness. Growth will require manufacturing new tissue, reproduction similarly demands the building of new individuals and persistence by means of repair or the general maintenance of homeostasis will have an associated energetic cost. All of these activities require direct input of energy and/or the intake of resources both as "fuel" and as raw materials for construction or repair. Importantly, to do more of any of these activities will require more such input, so fitness should scale with the consumption of energy and/or resources.

In short, then, the various fitness metrics we have looked at so far can be thought of as a disparate set of *outputs*, with the idea that they can be rendered commensurable via association with a *single input* required to generate all of them. If the input of energy or resources does indeed scale with the outputs associated with fitness, then it seems sensible to quantify the different outputs via the input required to generate them.

Consumption approaches have some immediately appealing qualities. For one, arriving at a singular fitness metric via this kind of "physicist's view" of the natural world helps to make sense of the intuition, mentioned above, that entities conducting the processes associated with fitness are fundamentally engaged in the same business – and does so in pleasingly mechanistic fashion.

Pragmatically, resource or energy use are both reasonably straightforward quantities to measure. Whilst not quite as easy as simply counting offspring, summing the resources or energy captured by an organism is a readily achievable proposition. Even as a less concrete phenomenon, energy is a well understood, ubiquitous physical quantity. Indeed, ecologists are already well accustomed to considering the passage of energy through ecosystems.

1.2. Note on Methodology

Before embarking on the main discussion, it will be useful for both this and the following chapter to clarify what I will *not* be discussing here. Especially in the current chapter, my focus above all else will be on deriving a viable fitness *metric* (as per the metric/measurement scheme/concept distinction in chapter two). Thus, I will simply be considering whether *any* measure based around resource or energy capture could be made to accurately track biological fitness. Such a radically disparate metric, beyond explaining how growth, reproduction and persistence relate, would also change how we think about fitness at a conceptual level – and I will discuss some of the implications the metrics I consider would have for our fitness concept. Crucially, though, my analysis here remains separable from concerns around measurement scheme. Thus, if we were to switch to measure fitness in terms of energy, we would need to determine the impact on our wider conceptual framework around fitness and selection. However, that switch would have no necessary impact on, say, whether we want to think about fitness as a propensity (as per Mills and Beatty 1979) or purely as a retrospective, "realised" quantity.

Similarly, I will not consider how any new unifying metric would interact with the issues in chapter three as to measuring fitness over time. The concerns raised there are logically downstream from questions over metric and I would expect the same problems to hold for any new metric or metrics just as they currently do for conventional numerosity metrics.

2. Van Valen

Whilst several authors examine various aspects of the natural world in terms of energy flow in particular (for instance Lotka 1922, 1944, 1945, developed in Odum and Pinkerton 1955 – also discussed in the next chapter), Van Valen provides a rare attempt to directly flesh out general accounts of selection and fitness in terms of both resource and energy flow. As such, his work provides a convenient point of entry to consumption accounts in general, with the pros and cons of Van Valen's theories largely representative of what we might expect for any similar approaches to fitness.

Van Valen's position is developed across several papers over a period of decades, beginning with his 1973, "A New Evolutionary Law" (see also Van Valen 1975, 1976, 1989). This is best known as the paper where he put forward his widely cited Red Queen Hypothesis, though that accounts for only a fraction of the content. Van Valen's work bursts with innovative ideas, but they are seldom fully developed or stated with complete clarity. Whilst he is relatively clear on foundational matters, a little interpretation is required to establish precisely what Van Valen intended and to set this out in systematic fashion.

We can extract two distinct, coherent accounts of fitness from Van Valen's work on selection. The first is what I will label his "basic account", where Van Valen (1973) regards fitness as realised through success in local resource competitions. The second, "advanced" account (developed in Van Valen 1975, 1976 and 1989) builds on this basic scheme and attempts to generalise it by proposing a single, global resource competition for the sun's energy (stored in various forms of "reduced carbon").

As we will see, the advanced account encounters significant problems not associated with the basic account (though that is problematic in itself). Therefore, it is maximally charitable to Van Valen to consider these two iterations of his thought separately. I will consider each sequentially before also providing some particular discussion on the need to conceptually underpin an absolute fitness measure to render it meaningful and how reference to competition fulfils this function for Van Valen.

2.1. "Basic Account": Resource Competition

From initially seeking to explain the regularity of the extinction rates amongst fossil species, Van Valen (1973) put forward the idea of zero-sum competition as the fundamental driver of natural selection, with this allowing competitive exclusion to explain observed constant extinction. Under Van Valen's account, competition will occur as entities struggle for share of a limited "resource space". As we saw in chapter one, such zero-sum conditions can lead to adaptive arms races. The constant adaptation required in order to keep pace in such circumstances leads to Van Valen's naming of the "Red Queen Effect" after a scene in *Alice through the Looking Glass* (Carroll 1872), where Alice finds she must run as fast as she can just to stay in the same place.

Under this scheme, we can measure the fitness of participants in any instance of selection in proportion to the share of resources they have sequestered for themselves. Thus, we might see organisms vying for grazing space and note that those increasing the area of land they control are fitter than those losing ground to competitors. We can then measure that fitness directly in terms of the land area occupied. The result is that Van Valen provides us with an account of fitness based on relative resource consumption.

Most importantly for our purposes, within the resource space being considered, different aspects of fitness are rendered commensurable. Whether the fitness of the entities concerned is manifested in terms of reproduction, growth, persistence or otherwise, these outputs are able to be compared via the common currency of the resource input required for each. In Van Valen's account, fitness is reflective of the resources consumed by an individual, as well as that individual's competitive ability in securing those resources.

This resource-based approach to fitness also brings other advantages. Notably, Van Valen's account greatly liberalises the groupings of entities which we can regard as undergoing selection alongside one another. Where involvement in an instance of selection is determined solely by participation in a certain resource competition, we can perceive members of different species as engaged in selection with one another and assign them fitness values which can then be compared across species boundaries. Thus, the Darwinian population (discussed in depth in chapter six) becomes defined relative to the contested body of resources – that is, to the resource space.

This idea makes a good deal of sense in light of some real biological cases, which look very much like selection, but cannot technically be designated as such under a standard approach, seeing selection as holding exclusively amongst conspecifics (often based on ideas of selection as a competition for representation in the subsequent generation's gene pool – which I argue against across chapters one and six). Consider a group of trees growing together in the middle of a dense forest. In such a setting, we are well accustomed to seeing the individual trees vying with each other as they strive towards the light they need for photosynthesis. This is a zero-sum contest in a very straightforward sense, in that trees will either push above and acquire sunlight whilst shading, and thus depriving, their peers, or they themselves will be shaded and deprived. We can even perceive the effects this competition has on the participants' phenotypes – especially in coniferous species, we observe the characteristic tall, thin, straight trunks, largely bereft of foliage except at the very top.

This behaviour occurs in the same way whether or not adjacent trees are conspecifics. A pine and a spruce will vie for light in much the same fashion as will two pines. However, under a standard approach to selection and fitness, only the intra-species case can be regarded as selective. This seems to make an arbitrary, "unnatural" distinction between phenomena that share precisely the same underlying causal structure. By contrast, Van Valen's account allows us to perceive selection in action, whether the competing trees are conspecifics or not, and measures their fitness relative to the amount of light they manage to capture.

This possibility of perceiving selection in whole new classes of scenario, accompanied by an appropriate fitness metric, would represent a significant expansion of explanatory scope for selective theory. By promising to hold in any case where entities can compete over a resource, Van Valen's account readily generalises to other levels of selection. One of the major problems in extending selection to other levels has been uncertainty over whether an appropriate analogue fitness measure is available. Measuring fitness in terms of resource or energy capture/consumption provides a solution to such problems and makes way for the valid extension of selective theory to explanatory roles where it is already frequently employed.

I have already discussed, in chapter two, how Okasha (2003) rules out the possibility of clade selection as a matter of definition. His rationale is that reproduction does not occur at the level of clades, meaning that selection simply cannot be perceived to act there. However, Van Valen's account validates already-common selective explanations as to clades spreading by outcompeting one another for resources. A typical example would be the account of how angiosperms (flowering plants) outcompeted gymnosperms, displacing them over the majority of global landmass (as in Brodribb, Pittermann and Coomes 2012).

This kind of resource-based approach to fitness would also readily generalise to substrates beyond the purely biological. For cultural evolution, regarding cultural units of selection in competition for resources such as "hosts" (mutually exclusive beliefs might compete for individual humans, whilst something like a song might compete for memory space or similar) would accord with remarks by Dawkins as to the importance of competition in cultural selection in his initial explication of memetics (for example, 2016:305-306), whilst also avoiding the well-reported issues around finding a satisfactory analogue to reproduction in the cultural sphere (discussed in Lewens 2018:§5).

Thus, we can see that even Van Valen's "basic" account has sweeping implications for our understanding of fitness and selection in general. If tenable, a consumption account of this type would provide a common currency between different aspects of fitness, within a Darwinian population defined by a specific resource competition. The same approach also promises to dramatically expand the explanatory scope of selective theory by allowing for inter-species selection and fitness comparisons and by offering opportunities for development in areas like cultural evolution.

2.2. Advanced Account: Energy, Universal Competition and Universal Fitness

Whilst Van Valen's basic account can allow for fitness comparisons across species boundaries, it still ultimately provides a relative, rather than absolute, measure of fitness. Fitness values will only be comparable between entities competing for the same body of resources (and thus within the same Darwinian population). However, Van Valen (1976) developed his idea of competitive selection further. Taking the idea that resources are ultimately a source of energy for the organisms exploiting them, he suggested that, in practice, all organisms on earth are in competition for a share of the sun's energy - typically stored as "reduced carbon".

Van Valen has it that all resources should be considered as constituent parts of a single pool of energy – and thus a single resource space. Technically, his new fitness measure is still relative to a single resource competition and a single Darwinian population defined relative to that competition. However, that competition, and thus Darwinian population, has now been expanded to take in all life on Earth.

The end result is to provide a single, universal fitness measure, allowing us to compare the fitness values of individuals previously regarded as participating in distinct, local competitions for different resources. In transitioning from Van Valen's "basic" to his "advanced" account, then, we have gained (in effect) an absolute, universal fitness metric. This creates a common currency between different aspects of fitness which could then be applied globally – not just to participants in a specific, local instance of selection. All this goes rather further than our initial goal in this chapter.

Van Valen's advanced account thus opens up a whole new realm of possible fitness comparisons beyond his basic account. If this kind of fitness measure could be made workable, it would represent a paradigm shift in evolutionary biology. This view of fitness is so radically different from any standard account that its full implications can be difficult to grasp. In his 1975 paper, "Life, Death and Energy of a Tree", Van Valen compares the fitness of a species of palm, *Euterpe globosa* to that of *Homo sapiens* and finds them to be roughly equivalent. Such a comparison, not just between species, but between trophic levels, allows for what seem like outlandish claims to be made – for example, that members of some carnivorous species might enhance their fitness by evolving to become sedentary photosynthesisers or vice versa.

Extending a fitness concept quite so far – to compare any individual under selection to *any* other – might seem to stray well into eccentricity – and I will deal with several problems arising from Van Valen's work shortly. However, there are some cases where this approach to fitness does accord with our intuitions and indeed seems to tap into matters of fact which we have no way to state within a standard framework. Thus, we might regard Van Valen's remarks about the relative fitness of trees and humans with suspicion, but some other inter-species fitness comparisons seem fairly innocuous and even obviously true. For example, we are accustomed to the idea that the common (brown) rat is an immensely successful species, and it would be fairly uncontroversial to say it was more so than, say, the giant panda. The idea of being able to state this insight in a more rigorous fashion and using the language of fitness might hold some appeal. As such, we might not be immediately dismissive of this possibility.

Now, having arrived at this point via his initial work on material resource consumption, it should be noted that Van Valen is not the only author to have approached the topic of evolution in energetic or related terms. As we will discuss in more detail in the next chapter, there is a lengthy tradition, running from Lotka (1922, 1944, 1945), through to more contemporary thinkers like Chaisson (2011) and Wicken (1986) of considering evolution directly in terms of energy consumption. However, work in this area tends to be concerned with macro-level trends in evolution (McShea 1998); with ideas that adaptation over time will drive up rate of energy flow or related quantities. Van Valen is alone in

providing a detailed development of these ideas at the "micro" level of fitness measurement. Thus, amongst all these authors, only his work is directly relevant to our concerns here.

2.3. Competition and Meaning

If it can be sustained, Van Valen's advanced account, in particular, offers incredible payoffs for selective theory. Indeed, these benefits should be available with any fitness concept providing a universal, *absolute* fitness metric (along with a suitable theoretical framework to support such comparisons conceptually) and is a theme we will return to in the next chapter. In light of what will follow, though, it is worth drawing explicit attention to the work done by zero-sum competition in underpinning Van Valen's advanced account and specifically his absolute fitness metric.

As noted previously, standard approaches will often measure fitness as a function of the frequency of a type within a population – that is, the percentage of the population accounted for by that type. The same organism might then be judged as more or less fit, depending upon the population in which they are placed. Fitness is thus relative to a specific Darwinian population and is thus not an absolute measure.

Many metrics could technically be *applied* in a universal, absolute manner. However, this does not mean it would be wise to do so or that the resulting values would be meaningful. In chapter two, we observed that none of the metrics put forward currently are singularly sufficient to account for all the cases we wish to regard as selective. If we ignore that issue, though, we could make an attempt to apply one of those metrics in a universal manner. For example, we could count numbers of individuals or measure biomass and compare the results across species. We could then say that a rat is fitter than a human as it leaves more offspring, or that a blue whale is fitter than either because it is heavier. The metric *functions* in this context in that one can count or weigh all these entities – the values can be arrived at. *However*, such a universal application is not supported by a theoretical framework to demonstrate that the comparisons are *meaningful*. It is not clear *why* number or size should be considered as a relevant comparison between species. The metric selected, then, must ultimately come with a conceptual underpinning to grant meaning.

Such a conceptual underpinning is always required, but this tends to be ignored in standard, numerosity accounts, where it is seldom explained why we should be interested specifically in the number of individuals as opposed to some other aspect of their success. Sometimes, vague reference is made to competition for representation in the next generation – though, again, I argue across chapters one and six that this is incoherent.

Van Valen arrives at an energetic fitness concept, having started from a competitive account of selection and then working all the way through to his advanced account. Technically, it is still relative to a Darwinian population defined via a certain resource competition. However, when the relevant resource competition expands to cover the whole globe and to include all terrestrial lifeforms as competitors, the resulting measure becomes an absolute one.

3. Problems for Van Valen and Similar Accounts

Ostensibly, large portions of Van Valen's work on selection and fitness make a good deal of sense. In particular, his approach captures apparent cases of selection between members of different species in competition (our trees vying for light) which a standard account cannot accommodate. However, on any rigorous consideration of the scheme, a whole swathe of conceptual problems soon emerge. Van Valen's work is doubly useful to us here in that it anticipates and provides partial response to the kind of issue I raise. Such response can thus be employed on behalf of consumption accounts generally. However, I will show that Van Valen's attempted resolution falls rather short of being sufficient to salvage his approach to fitness measurement. Whilst I will later argue that we can salvage some useful ideas from Van Valen's work, both versions of his account, as he proposes them, are fundamentally untenable.

Multiple chapters could easily be expended in critiquing Van Valen's scheme. For our purposes, though, it will be sufficient to draw attention to a salient subset of problems. Specifically, these will be problems that we can expect to generalise to any similar account deriving a resource and/or energy consumption-based fitness metric.

First, I will address concerns related to the role of competition in Van Valen's account. Competition is not a *necessary* component of a consumption-based fitness metric, but it does provide the conceptual underpinning for Van Valen’s account and is similarly foundational in various other energy-based treatments of evolution (for example, Boltzman 1886, Lotka 1922, Chaisson 2011).

Given that competition is indeed strictly unnecessary for a consumption view of selection, the group of issues I label “efficiency problems” will be much more damning for energy or resource-based accounts in general. Such consumption accounts require a reliable relationship between “input” of energy/resources and “output” in terms of increased fitness. I show that this relationship is not, in fact, reliable due to “inefficiencies” between input and output. As such, these critiques made of Van Valen's

account will be just as relevant to any similar energy or resource-based fitness metric, regardless of how it relates to competition.

Finally, I note the problem for any consumption account of fitness in dealing with systems where there is no energy or resource flow – that is, in dealing with entities that have no metabolism or are considered "non-living". Rather than accounting only for "niche" or tenuous instances of selection, I show that there are cases where we would very clearly want our theory of selection to apply to such systems.

3.1. Competition

Both variations of Van Valen's theory lean heavily on the idea of zero-sum competition. His basic account requires all cases of selection to be driven by some form of resource competition, whilst his advanced account relies on a single, global competition for energy. As noted, other energy-based approaches to evolution have also tended to be couched in terms of competition.

As discussed in chapter one, many cases of selection are indeed driven by zero-sum resource competitions. In such cases, resource or energy capture might reliably track fitness, and it can seem like a natural step to build a view of selection and fitness on this foundation. However, any consumption account of fitness will run into serious issues where it is reliant on ideas of competition – which I examine here.

3.1.1. Selection is Not Always Competitive

In chapter one, we found that zero-sum competition is not a necessary component of selection. I showed that selection driven by zero-sum competition was only a subset of the wider category I defined as cases of "strategic" selection - which was itself defined in opposition to the further category of "parametric" selection. Illustrations of non-competitive, but still clearly selective, scenarios were given as examples of these other modes of selection (for instance, a population afflicted by a new disease will not be in competition against one another to survive, but rather will simply live or die based on their individual resilience to the pathogen).

Whilst Van Valen's advanced account proposes a speculative global competition for energy, even his basic account rests on the assumption that selection in general will be driven by resource competition at a more local level. As we have discussed, in the absence of competition, Van Valen's fitness metrics, as he proposes them, lose their meaning. If selection does not entail zero-sum competition, both the basic and advanced account are untenable, as will be any related consumption account of fitness rooted in a competitive view of selection.

3.1.2. Global Competition is Implausible

Even if it were feasible to ignore exceptions and to limit natural selection to cases including zero-sum competition, the fact remains that the *global* resource competition which underpins Van Valen's advanced account is not empirically plausible. If the kind of worldwide resource competition Van Valen's account requires were in force, it would have real implications running counter to what we observe in nature.

The absolute fitness values Van Valen hopes to ascribe gain their universality by means of an apparent contest of all against all for the energy of the sun – either absorbed directly or stored in forms of "reduced carbon". However, when we look at the empirical world, even the mere facts of geography make the operation of such a competition difficult to imagine. Are we really to believe that a human from the United Kingdom is in competition with an antelope in China? Even at the same trophic level, is a shrub in South Africa really to be regarded as in competition with one in Canada? Surely, the individuals concerned are too causally isolated for any meaningful competition to hold (see Lewens 2010:831 for a similar discussion).

Initial impressions, then, strongly suggest that there will be a fractured multitude of separate competitions going on across the globe. Importantly, this is also borne out in observed reality. Thus, we can compare differing empirical implications which would result from a single resource competition being in operation or not. Which of these images of the natural world is correct is ultimately an empirical question – and the empirical evidence favours the "common sense" position of multiple competitions.

Under Van Valen's universal competition, we would consider a species that has been successful in terms of resource capture in one area to be successful generally. If competition was really in operation globally, then the amount of energy controlled would represent an absolute measure of fitness. In this context, fitness is an absolute measure of competitive ability in sequestering energy, so should predict the outcomes of future competitive pairings. If Van Valen were correct, organisms that are successful in one region should be just as well adapted to their ecological niche as those that are equivalently successful in similar niches in other regions.

Where competition was fractured into local resource competitions, though, being competitively successful can only imply anything about fitness relative to the competitors which have actually been faced locally. The fact that one has won a contest against one specific set of competitors is no guarantee that one will continue to win when that set of competitors is changed. As such,

in the case of such "fractured" competition, current realised fitness in terms of resource capture will not predict the outcome of future competitive pairings.

Widely reported problems experienced with invasive species provide us with clear examples of precisely this phenomenon, whereby current fitness in one locale will not predict how an organism fares in competition with individuals arriving from distant locales. Invasive species tend to pose problems in smaller ecosystems that have been isolated for significant periods of time. As such, the species that are dominant in different niches might simply have been the most competitively able of a relatively small number of contestants – and so might not actually be especially well adapted to that niche in absolute terms. In less isolated regions – across large continents, for example – more species will emerge and compete with one another in any given niche. This should mean that the dominant species in a particular niche has been selected as the ablest of a much larger number of contestants (See Elton 1958 for an initial statement of similar ideas, and Richardson and Pyšek 2007, Fridley et all 2007 and Moser et al 2018 for more contemporary assessments)

Often, then, when human intervention or other phenomena bring new species into isolated ecosystems, we see the native species rapidly displaced by more competitively able types, better adapted to the relevant niche. One well-reported example concerns the highly isolated fish population in Lake Victoria. The lake was populated relatively recently, in evolutionary terms, by cichlids which had subsequently undergone incredibly rapid adaptive radiation to occupy the various available ecological niches. However, the Lake Victoria cichlids have been devastated by the introduction of the Nile perch to the region in the 1950s – with the new species intended for commercial fishing. The Nile perch had been evolving to thrive in a similar niche to many of the cichlids for a much longer time and, as a result, proved a much more efficient hunter than many of the predatory cichlids, outcompeting them for food, as well as directly preying on other cichlid species. The result was that hundreds of species of cichlid became extinct (Pringle 2005).

Similar examples are found across the world, with particularly famous cases in New Zealand (Clout and Lowe 2000) and Australia (Hoffman and Broadhurst 2016), where invasive species have caused enormous, well-publicised problems for native ecosystems. The shock caused by these new species is visceral proof of the fact that there is potential for significant de-linkage between success in local resource capture and competitive ability against successful types in other locales. In turn, then, this clearly demonstrates that the kind of global resource

competition relied upon by Van Valen's advanced account (and similarly envisioned by Lotka and others) is not in operation.

3.1.3. A Weaker Form of Competition?

The reader might think that I have applied an overly strong notion of competition and have held Van Valen's work and, by extension, similar theories to an unrealistic standard. After all, surely, he could not have meant to make such an implausible proposition? Briefly then, we can consider the possibility of a weaker form of global competition.

To construct a more believable model of how competition could span the globe, we can imagine that individuals are only in direct competition with their immediate neighbours. Notwithstanding my points in chapter one about selection often occurring without zero-sum competition, this seems reasonable enough. Now, the fact that those neighbours compete with their own neighbours lets us envision a chain of competitive interaction which would stretch across the globe without implying direct competition between individuals that are obviously causally isolated from one another. If we have individuals A, B and C arranged along a line in space, then, A would compete with B and B with C, but not A with C. Thus, we can think of all three being part of one competition without supposing that A and C are actually direct competitors. This would be equivalent to the rationale which regards all the members of a ring species as part of the same gene pool, despite the fact that individuals geographically far removed from one another are physiologically unable to successfully breed together (Ridley 1996:47-49).

Unfortunately, competition, treated as a transitive property in this fashion, is not enough to allow Van Valen's account to function. This is because competitions for the same resource can be won by different means. For example, A might beat B by having better vision, but B may beat C by being more aggressive. This does not tell us which would win if A and C found themselves in competition – it might be that C beats A by being better camouflaged, by having a more efficient metabolism, or by any number of other means. This is analogous to a human game of rock paper scissors. Scissors may beat paper and paper may beat rock, but scissors do not beat rock (Sinervo and Lively 1996 describe exactly this form of competition in the side-blotched lizard)

Even allowing for the most charitably weak form of competition, then, Van Valen's advanced account cannot be made plausible. Therefore, we can conclude an exhaustive proof that any consumption account of fitness cannot rely upon ideas of competition. This is damaging not

only to Van Valen, but to related accounts from Boltzman (1886), Lotka (1922) and Chaisson (2011) which similarly refer to competition.

Of course, given that numerosity-based accounts of fitness seldom explicitly provide this kind of conceptual foundation themselves, we could say that my criticism here simply brings Van Valen's account down to the level of those more typical accounts – and so cannot be held against Van Valen. Thus, we might describe this particular aspect of our analysis as ending in a "nil-nil draw", as both the status quo and Van Valen's account come with issues around their conceptual underpinning. In any case, more damaging objections to consumption accounts in general are provided by the set of "efficiency" problems, to which we now turn.

3.2. Efficiency Problems

There is no strict necessity for a consumption account of fitness to be based on ideas of competition. However, even if we assume that we can indeed flesh out such a treatment of fitness without reference to competition, we will still run into a host of problems. In particular, there is a set of interrelated issues I refer to as "efficiency problems", to which any consumption account of fitness will be inherently vulnerable, independent of its specific formulation. This is a group of problems whereby energy and/or resource consumption have the potential to significantly de-link from an entity's fitness. I chose the term "efficiency problem", then, as issues arise from the possibility of an imperfect and variable correspondence between energy input and fitness output. Thus, we can think about efficiency in fitness production as similar to the efficiency of a machine in transforming energy into useful mechanical work. Many iterations of the same basic problem are possible, though I will limit discussions here to a crucial subset. For simplicity, I will discuss the matter of efficiency primarily in terms of energy, though the same points can be made in terms of resource consumption.

3.2.1. The Same Energy Can Be Used for Different Processes

Both iterations of Van Valen's approach to fitness rely on either energy or resources to act as a common currency between the disparate fitness-relevant outputs of different individuals. However, this requires an underlying commitment to the idea that the consumption of energy or resources will always translate to fitness at the same rate. We can think of this as the idea that "spending" resources or energy will "buy" fitness at the same price. Thus, we must be able to suppose that the consumption of x quantity of energy or resources will yield y increase in fitness in all cases. Indeed, this is a foundational commitment that seemingly must underlie any viable consumption account of fitness – which will inherently rely upon robust correspondence between input and output.

However, the assumption that energy will always confer fitness at a single rate is unjustified for several reasons. Perhaps the most obvious of these is that the energy consumed by any organism might be put to use in any number of different processes within that same organism. We have no good reason to expect that each of these processes will positively contribute to fitness at all, let alone how directly, and should expect significant variation in this regard. For example, energy directly spent on generating new offspring will not necessarily confer the same fitness per joule as that spent on foraging, nest building or mating displays – even if all are ultimately essential elements of the organism's complete life cycle. Indeed, because they are all essential parts of a life cycle, the relevant organism will *have* to conduct all of them, even if some of those processes represent a relatively poor return of fitness for energetic investment. For example, an organism cannot feasibly put all its energy directly into reproduction at the complete expense of foraging for food. In short, it seems highly improbable that the different processes organisms engage in will all "buy" fitness at the same rate. We can thus say that different processes will likely transform energy to fitness with different efficiencies. Indeed, it seems that we should anticipate that the overall "efficiency" of conversion between energy and expected fitness will vary as energy is used by organisms in different ways.

Usefully, Van Valen shows some awareness of this issue and seeks to address it via his idea of "expansive energy"; whereby he partitions one category of energy use to be associated with fitness. The idea is that expansive energy is that fraction of the energy at an individual's disposal *directly* utilised in fitness-related activities, such as reproduction or growth. This avoids having to worry about other processes at all. The full taxonomy of different kinds of energy use Van Valen (1976:185) describes is as follows:

> Total trophic energy controlled = e_c
>
> $e_c = e_d + e_w + e_r + e_s$
> $e_d = e_m + e_e$
>
> Where:
> e_d = directly productive energy
> e_m = maintenance energy
> e_e = expansive energy (fitness)
> e_w = waste energy
> e_r = reserve energy
> e_s = structural energy

Leaving aside plausible concerns about so readily discarding activities like maintenance as important contributors to fitness (especially if we consider persistence to be an aspect of fitness), there are more immediate problems as to how anything like an expansive energy concept could be coherently defined. Major issues arise as to whether we are to measure expansive energy as a momentary flux or whether it can be stored – and, if so, how it can then be differentiated from "reserve" or "structural" forms of energy. Van Valen seems confused on such issues himself. He initially defines expansive energy in terms of momentary flux, but later goes on to discuss expansive energy as something which can indeed be stored, with the phrase "fatness is fitness" coming to be associated with his scheme (Van Valen 1989).

These considerations aside, though, the fundamental problem for the expansive energy concept, from an "efficiency" point of view, is that it might narrow down the number of different processes upon which energy can be spent in relation to fitness, but it does not reduce that number to one. Thus, expansive energy might still be spent on a variety of processes (all those associated with growth and reproduction, for a start) without us having any idea of the rate at which energy buys fitness in each.

The fact that species are adapted to favour growth or reproduction in different contexts (as described by Harper 1977, Bouchard 2008 and Janzen 1977 and discussed in chapter two) clearly demonstrates that even these directly fitness-enhancing activities do *not* contribute to fitness at the same rate in a given environment. As such, Van Valen's expansive energy idea might reduce the fundamental problem here, but that problem remains nonetheless.

Beyond this, it is also notable that holding fitness as relative to expansive energy would have the effect of de-linking Van Valen's fitness concept from competitive performance. At a higher level, transitioning to anything like an expansive energy concept effectively moves away from a "consumption" account and back to considering entities' fitness-relevant "outputs" (growth, reproduction etc) directly, as per standard fitness metrics. Van Valen's approach would then be set apart only by imposing energetic cost as a common currency between those disparate outputs.

Thus, it would be possible for an entity to capture more total energy than a competitor – that is, to be more successful in competition – but be considered less fit because they make use of less of that total as expansive energy. This would cause conceptual issues for Van Valen's or any similar account where measures derive their significance from linkage to competitive performance. I will not pursue this issue further here, though.

3.2.2. The Same Process Can Be Conducted With Different Efficiencies

The conceptual issues around trying to partition different uses for energy via any relation to Van Valen's expansive energy concept are many and likely intractably complex. Instead of pursuing an analytic blind alley, though, we will shift focus to another iteration of the same general "efficiency" problem. This is both a problem in its own right, whilst also negating the need to fully analyse the expansive energy concept by showing that the approach it represents is generally untenable.

Thus, let us imagine we somehow came up with a much-improved version of something like Van Valen's expansive energy concept, which successfully limited the number of processes associated with fitness to just one (perhaps something like the construction of tissue across reproduction, growth and repair). The fact is that this would *still* be subject to efficiency problems.

To explain, we have already noted that different processes might yield fitness at different rates. The expansive energy concept promised to account for this by narrowing down the range of different processes for which energy throughput was associated with fitness. Thus, there would be less to worry about regarding how energy might be partitioned between more or less fitness-enhancing activities where we have drastically reduced the number of those activities in which we are interested. However, even if we were notionally able to take this to the extreme and associate fitness with one single, energy-consuming process, it would remain entirely possible that this same process operated at different efficiencies in different individuals.

We might refer to any number of possible examples of variation in efficiency. In many contexts, we might expect that evolution will bring forward ever more efficient ways of achieving the same ends. Thus, we would anticipate differences in the efficiency of everything from basic metabolic processes to the manufacture of specific pigments, enzymes or toxins. Those individuals deriving more value in return for their energy expenditure – "more bang for their buck" – all things being equal, would tend to derive a selective advantage by doing so. Even in the human case, we are anecdotally well accustomed to the idea of individuals having different metabolic efficiencies – we all know some people who struggle to keep weight on no matter how much they eat and those who struggle to keep it off. The perverse fact for humans in developed nations is that constant surplus food availability means that it is inefficient metabolisms which we would expect to be selected, since their owners would be less likely to become obese with over-eating.

This de-linkage between energy input and fitness output becomes especially pronounced when we include cases where fitness-related processes recruit what might be thought of as an "extended phenotype" (Dawkins 1982). Compare, for example, two types of crab. One goes through the normal, energetically expensive, business of growing its own shell. The other, however, does as the hermit crab and simply finds and inhabits a vacated shell produced by another organism. The end result is the same, in that the crab is furnished with a shell to protect against predation and the other rigours of its environment. On one analysis, both kinds of crab exhibit a means of generating a shell for themselves, with both processes being energetically costly to some degree; whether growing a shell or foraging for one. However, the process of locating an existing shell realises the same outcome for a much smaller amount of energy. All things being equal, our “opportunist”, hermit-type crab will reap a higher reward in terms of fitness per joule of energy expended. Energy consumption, then, is again shown to de-link from fitness via another efficiency problem.

3.2.3. Energy Might Be Useful Only in Discrete Amounts

Now, let us imagine that we could (implausibly) narrow down our consideration of fitness-enhancing energy expenditure to one single process and that this process was identically efficient between organisms, such that the same input energy would always yield the same output result. Thus, we would expect that 1000 joules of energy would yield the same outcome when used by organism A as for organism B. This unrealistically charitable case avoids all the problems above. However, we might *still* run into problems in practice. This is due to a slightly different kind of efficiency-type issue, emerging from possible non-linear relationships between energy input and productive output. This idea will need a little explanation.

To make an illustrative analogy, in the early days of quantum physics, it was realised that the electrons surrounding atoms could only occupy certain discrete orbits. To excite an electron up from one orbit to another, a certain minimal amount of energy was required, corresponding to the energy difference between orbits. If the energy input was equal to or higher than this value, the electron would move to the higher orbit. However, if the energy input was smaller than the energy difference between orbits, then the electron would stay put. Crucially, there was no middle ground. Supplying half of the energy required to excite the electron would result in no change to its orbit; as would supplying 95% of the required energy. The insight, then, was that that energy will be useful in discrete quantities, with inputs below certain threshold levels failing to yield any effect at all, regardless of their value.

As below, so above, and we often find qualitatively similar phenomena at the macro-level of the biological world, where non-linear relationships hold between input and output. For example, for an individual engaged in reproduction, we can expect that there will be a certain minimal energetic or resource cost per offspring produced. This is the cost associated with requirements such as the manufacture of eggs, provision of post-natal care and/or carrying a pregnancy to full term in viviparous species. Returning to our imaginary organisms above, 1000 joules might yield the same output for both A and B, but if B now has 2000 joules, there is no guarantee that it will gain any additional fitness *at all*. Certainly, we cannot assume that 2000 joules will be twice as useful as 1000 joules.

In our example, an organism can either make the full minimum investment required to create one viable offspring, or have no offspring. There is no middle ground, as viable offspring cannot be produced in fractions. Half the required investment will result in zero offspring, not half an offspring. Similarly, for an individual on the verge of starvation, acquiring food at 95% of the minimum rate necessary to sustain life will not be 95% as useful as the full amount, as death will be the inevitable result of acquiring anything less than the minimum requirement for subsistence. Thus, we observe a non-linear relationship between energy input and fitness output, making for another potential source of "inefficiency" between the two.

The adaptive effects of such non-linearity can be readily observed. For example, this phenomenon explains the asynchronous egg hatching observed in some bird species (Lack 1954, Skagen 1988). In such species, the eggs of a single clutch will be laid and incubated so that they hatch with a certain time delay between each, rather than all at once. This means that the resulting chicks will grow to maturity one by one, rather than simultaneously. Consequently, rather than all the chicks maintaining approximately the same size as one another as they mature together, there will be a spectrum of sizes amongst them – a largest, a smallest and a range in between.

This difference becomes important as food becomes scarce. Where chicks are the same size, their equally matched competition for food delivered by the parents will mean that each receives a similar share. As food supply diminishes, though, the equally divided amount each chick receives will be reduced until it falls below the critical value needed to maintain life. At this point, all the chicks will die and the whole clutch is lost.

However, where chicks are of different sizes due to asynchronous hatching, the largest will be able to command a greater share of incoming food than the smaller chicks, with the ultimate

result that, as food supply diminishes, chicks will die off one by one, from the smallest to the largest, stopping when the remaining number of chicks can be sustained by the food available. Thus, the number of chicks in the clutch automatically adjusts to maximise the number which can be fledged with the available resources, rather than run the risk of losing the whole clutch. As such, we have an example, not only demonstrating the fact that fitness will not necessarily scale linearly with energy or resource consumption, but also of the emergence of adaptation which functions to help mitigate this effect.

Though we can see that this consideration influences the evolution of reproductive strategies, one might speculate that the kind of non-linearity we have observed will not be of enormous significance in many cases and, indeed, that it might average out over a sufficiently large population. However, over a whole population, the effect will not converge on zero; as we would expect for the influence of drift, for instance. Rather, some reliable fraction of total energy or resource consumption will be wasted as a result of the non-linear relationship between input and output. The outcome, then, is that we can list an additional source of "inefficiency" between energy or resource input and fitness yield.

3.2.4. Implications of Efficiency Problems

We have seen that there are many cases where we can expect that the energy or resource consumption of individuals will fail to track their fitness. The problems identified here are sufficiently fundamental that they will generalise well beyond Van Valen's work to any account of fitness measuring biological success via "consumption". Indeed, it is worth explicitly restating that, despite my tendency to focus on energy in my points above, the same criticisms will also apply to fitness measured in terms of resource consumption. Both forms of consumption account will ultimately depend upon a reliable correspondence between input of either resources or energy and output of fitness.

Of course, what I have said here does not preclude the possibility that consumption accounts might accurately track fitness in some systems - particularly those having adapted over time to operate at high efficiencies. However, selective theory must also allow us to chart how evolution *arrives* at such optimised forms in the first instance, and so must apply to the sub-optimal, inefficient entities that preceded them. Such "wasteful" systems will thus necessarily remain a subject of our interests and must be accommodated by theory.

As an aside, it is worth noting that it was important to deal with competition alongside efficiency problems, as the former would potentially offer a solution to the latter. Thus, a

competitive consumption account could make the claim that resource or energy capture can track fitness simply as a reflection of competitive ability, rather than as a proxy for output in terms of activities like reproduction or somatic growth. Under this approach, outputs in terms of growth, reproduction or persistence could be largely forgotten, as input is not a means to, or proxy for, success, but straightforwardly demonstrative of success *in itself*. However, by removing any possible recourse to competition, we make sure that criticisms based on efficiency find their mark.

3.3. Selection in Non-Living Entities

Aside from efficiency problems, another fundamental issue afflicting any "consumption" account is the inherent limitation it imposes on the kind of system with which we can associate fitness values. Specifically, measuring fitness as any function of the consumption of resources or energy means that we can then only measure fitness in systems with a flow of such resources or energy through them. Depending on one's preferred definitions, these are entities that might be labelled as having metabolisms or, in line with Schrödinger's definition (1944, discussed in the next chapter), being living beings.

Ostensibly, this might not seem overly problematic – we typically like to think of selection occurring between life forms anyway. However, even leaving aside possible cases of the selection amongst computer viruses, artificial life or units of culture, there are many less-exotic scenarios where we might very well want to perceive selection amongst entities without a clear metabolism or energy/resource flow focussed on them.

As a good example, the definition of life literature will often deal with ideas of dormancy or cryptobiosis as states somehow between life and death (Jeuken 1975). Many organisms can become dormant, suspending metabolic processes for long periods of time before returning to full life whenever conditions are right. Tardigrades provide a wonderful illustration from the animal kingdom (Guidetti, Altiero and Rebecchi 2011). However, I will consider the rather less exotic example of seeds. Let us say that some species of plant disperses its seeds in autumn. These seeds lie dormant in the soil over winter and germinate when the temperature rises in spring. Let us then suppose that winter was especially harsh and that freeze-thaw damage destroys certain seeds with thinner coatings. Only those seeds with thicker coatings then manage to germinate in spring.

In this case, we would probably say that selection has occurred and has selected for thicker coatings. One might argue over the conceptual distinctions as to whether dormancy is somehow a subset of life or not (Jeuken 1975) and it would be possible to contend that our seeds will be associated with future

energy flux when they germinate in springtime. To these points, I would respond that what is important is that we recognise selection itself to have occurred at a time when the seeds had no energy throughput associated with them. Either way, though, it is quite possible that we would want to consider selection between permanently non-metabolic entities, where it is difficult to associate energy flux at any time. This would be useful in considering selection between prions (Weissman 2012, Shorter 2010) or similar in the biological realm or in dealing with cultural selection. Neither iteration of Van Valen's theory, nor any other energy-based metric, can measure fitness in such cases of selection, and the issue will generalise to any similar consumption-type account.

4. Where Next?

I have shown that there is a set of fundamental problems which render Van Valen's or any similar approach fundamentally untenable. However, we must avoid throwing out the baby with the bathwater. Rather, we should recognise that Van Valen's general approach is not without some merit. Crucially, tackling the subject of fitness in terms of the underlying physical reality does seem to get at the correct *kind* of commonality between the different fitness metrics considered in chapter two, satisfying our strong intuitions that growth, reproduction and persistence really are fundamentally similar.

Both iterations of Van Valen's account also allow for somewhat radical and very interesting inter-species fitness comparisons. Some of these, such as comparing the fitness of a human and a tree, might seem outlandish. However, others are not only plausible, but allow us to account for apparently valid selective scenarios that are simply ruled out by conventional approaches to fitness. I noted the potential to give rigorous foundation to the strong intuitive impression that the common rat was a fitter lineage than that of the giant panda. A related example was that of clade selection, where Van Valen's more permissive scheme seems to capture reality better than a conventional approach to fitness and selection – as exemplified in Okasha's (2003) dogmatic treatment of clade selection.

These permissive fitness comparisons mean that Van Valen's account will necessarily interact with the Darwinian population concept (discussed in chapter six), which would have to be adapted to accommodate our regarding new groupings of entities as under selection together. Thus, we also have the promise of new theoretical development in that area.

Generally, we might discard Van Valen's work as fundamentally flawed but are left with the feeling that we have come close to an account of fitness which would yield substantial gains both at the conceptual level, in terms of better capturing reality, and at the more pragmatic level of increasing the

explanatory scope of our theory of natural selection. The question, then, is how should we go about trying to salvage some of the advantages of Van Valen's approach?

The most fundamental issue facing any kind of consumption approach to fitness is the set of "efficiency" problems, which expose the unreliability of consumption as a proxy for organisms' fitness-relevant outputs. This is then compounded by our realisation from chapter one that competition is not a universal feature of selection. Not being able to refer to competition in all cases precludes focussing simply on consumption as an indicator of fitness as competitive ability. The inability of consumption accounts to capture selection in non-metabolic systems is also a problem.

Going forward, then, it seems worthwhile to continue to explore a "physical" approach to unifying disparate fitness metrics, but to re-focus on the side of output rather than consumption. Whichever metric we move towards should also be meaningful without reference to competition, so as to capture non-competitive instances of selection. Energy itself might not be the best quantity to employ as a metric, given its unsuitability in dealing with non-metabolic systems. However, we should ideally pursue a similarly universal metric, so as to inherit at least some measure of the increased explanatory power promised by Van Valen's work. I will pursue this approach in the next chapter.

Conclusion

In this chapter, I sought to address issues raised in chapter two. My metric-pluralist position there raised questions as to what the different aspects of fitness identified held in common, as well as the related possibility of deriving a common currency between them. This proposition seemed particularly promising given our strong intuitions that the identified components of fitness – growth, reproduction and persistence – seemed to be closely related phenomena, despite their failure to reduce to one another.

Whilst far from the mainstream, Van Valen's approach offered ready-made solutions to these issues, elaborating fitness in terms of the consumption of both essential resources and raw energy. Van Valen's work was taken as representative of what I grouped as "consumption" accounts in general. Unfortunately, I demonstrated that a reliance on ideas of competition, "inefficiencies" between consumption and fitness-relevant outputs and the inability to accommodate selection in the absence of metabolism combine to render Van Valen's, and any similar consumption account, fundamentally untenable.

However, I noted that aspects of Van Valen's work remain promising. The attempted unification of the disparate fitness metrics of chapter two, in terms of energy use in particular, seems to *approach* the truth, despite ultimately missing the mark. The greatly liberalised capacity for fitness comparisons offered by Van Valen's approach captures many instances of selection better than conventional accounts, whilst also promising to greatly increase the explanatory scope for our theory of natural selection. We should not give up on these potential conceptual and explanatory gains. Thus, in the next chapter, I sketch my own attempt at deriving a unifying fitness metric, aiming to build upon what is good in Van Valen's approach, but without inheriting the same problems.

V

A THERMODYNAMIC APPROACH TO FITNESS

In this chapter, I will sketch my own approach to fitness in response to the problems we have encountered up to this point. Thus, I will propose that we consider fitness in thermodynamic terms. I will begin from Schrödinger's characterisation of life as a local inversion of the second law of thermodynamics, maintaining or accumulating negative entropy over time. Thus, I suggest that we should associate biological success with the magnitude of that characteristic behaviour. Fitness would thus be a function of the maintenance or accumulation of negative entropy over time.

I find that this allows us to conceptually, if not quantitively, unite the disparate fitness metrics we have considered previously as local proxies for negative entropy. In doing so, we are also able to achieve the significant outcome of uniting our concepts of life and fitness. This position both follows from my analysis up to this point and also fits within an existing tradition of thermodynamic approaches to the biological world.

This chapter builds directly on chapters two and four. In chapter two, we arrived at a metric-pluralist stance regarding fitness. Metric-pluralism offered significant advantages over conventional monist, numerosity-based treatments of fitness as well as over dissident theories proposing replacement monist metrics. However, aspects of the metric-pluralist stance left certain important questions open. In particular, a strong intuition exists that the metrics we have looked at so far – numerosity, biomass and persistence – do indeed have something fundamental in common. This then pointed to the possibility of deriving a singular "common currency" metric, which would render the different aspects of fitness commensurable. Beyond this, the metric-pluralist account was in need of a conceptual underpinning that could answer the related questions as to what exactly the disparate fitness metrics we had considered held in common and how we would decide whether any proposed additional metrics were valid ones. Thus, we wondered what was shared between numerosity, biomass and persistence and what it would take for additional metrics to be added to that list (in more abstract terms, we were left curious as to the membership criteria for the set of valid fitness metrics).

After expanding my pluralist approach to fitness measurement into the temporal dimension in chapter three, I returned in chapter four to address these issues. I noted that there was a tradition of what I

referred to as "consumption" approaches to selection which – whilst far from the mainstream – provided an off-the-shelf approach to tackling the questions in hand. Van Valen's work presented a well-developed example of a consumption approach to fitness.

Via analysis of Van Valen's work, I established that such consumption approaches were fundamentally flawed. Major issues were identified around reliance on competition to render fitness values meaningful, "efficiency" problems – where consumption as "input" failed to reliably track fitness as "output" – and the inability of consumption approaches to capture selection in non-metabolic systems.

All this said, I noted that Van Valen's general approach was not without its merits. Most notably, we explored the great increase in explanatory scope for selection which would accompany a unifying "common currency" fitness metric. The explanatory payoffs from the absolute fitness measurements promised by Van Valen's "advanced" account were most profound, with these allowing for particularly radical, unconventional fitness comparisons. Whilst resource and/or energy consumption ultimately failed as a suitable basis for measurement, Van Valen's work did seem to approach something like the truth more generally, and the broad line of enquiry is worth pursuing.

This leads me, in this chapter, to sketch my own unifying account of fitness. Though my treatment will retain something of the spirit of Van Valen's work, I will aim to avoid the problems associated with consumption accounts, whilst preserving as many of the benefits promised by Van Valen as possible.

To summarise then, we are effectively setting out with something like a "shopping list" of requirements and aspirations. To be successful, my account should grant the following:

- A common currency metric to render the different fitness metrics of chapter two commensurable.
- That this metric is quantitative and readily measured – as was resource or energy consumption.
- A conceptual underpinning to make sense of the multi-faceted nature of fitness observed in chapter two.
- That this conceptual underpinning not be reliant upon reference to competition.
- That we avoid efficiency problems by assessing fitness via "output" rather than "input".
- The possibility of selection in non-metabolic systems.
- Ideally, an increase the explanatory scope of our theory of natural selection by allowing for more permissive comparisons of fitness than are currently workable.

This will give us something to measure my own proposed account of fitness against. That account will indeed build upon Van Valen's manner of thinking about fitness in terms of fundamental physical quantities, but seeks to improve on that treatment significantly. In doing so, I will structure this chapter as follows:

1. Selection and the Second Law

I start from the ground up, examining the commonalities between reproduction, growth and persistence in the most fundamental terms. Thus, I find that the activities associated with fitness seem to strongly echo the thermodynamic definition of life associated with Schrödinger. As such, I propose pursuing a thermodynamic account of fitness, seeking to track negative entropy.

2. Provenance

The idea of a "thermodynamic" approach to fitness might seem eccentric to many readers. Thus, I demonstrate that there is already a long history of considering the phenomena of both evolution and life in thermodynamic or related terms. This discussion is intended to normalise my approach, whilst also highlighting a body of literature to be drawn upon and that my account here can be regarded as developing.

3. Sketching a Thermodynamic Approach to Fitness

I begin by outlining the general form of my proposed thermodynamic approach to fitness. However, I note that extended elaboration of this theory jumps the gun when we have not yet set in place a functioning fitness metric. Given that some means of measuring negative entropy will be an essential component of any such metric, I then move to focus on this most fundamental issue.

4. Deriving a Metric

Starting from the characterisation of life we derive from Schrödinger and subsequent authors, I note that there are two major routes by which we might attempt to measure negative entropy or generally the "extent" or "magnitude" of this kind of system. The first is via the flux of something like energy, resources or negative entropy through the system, though I note that we have already ruled out this option in the last chapter. The second route is via a more direct measurement of the negative entropy of the system itself.

The existing literature on thermodynamic approaches to evolution contains several measures purporting to measure entropy in a biological context. However, I note that these accounts are not appropriate to our goals, as they offer intensive rather than extensive measures and attempt to capture large scale trends in evolution, rather than the "micro" level activity of selection.

5. Prospects for a Useful Measure of Negative Entropy

Since an appropriate, extensive measure of negative entropy is not available off-the-shelf, I examine the prospects for deriving one. Via a discussion of the fundamental nature of entropy, I find that the current prospects for a functioning measurement are bleak. Even if such a measure were possible in principle, I note that it could not be usefully applied.

6. Implications

The failure to derive a functioning quantitative measure for negative entropy means that we will not be able to arrive at a unifying "common currency" thermodynamic fitness metric. In terms of actually measuring fitness, then, we will be forced to fall back to the metric-pluralist position arrived at in chapter two. The kind of radical, quantitative fitness comparisons promised by Van Valen's advanced account are thus also rendered impossible.

However, we are far from "back where we started". Even without a quantitative measure for negative entropy, a thermodynamic approach to fitness can still do much positive work at the conceptual level. I show that my account can still fulfil many key points from our "shopping list" above, whilst offering significant theoretical advance by uniting the concepts of life and fitness.

On final analysis, I find that, whilst a thermodynamic approach to fitness cannot be everything we might have hoped, it still represents a significant step forward, as well as providing fertile ground for further work.

1. Selection and the Second Law

At the end of chapter two, I noted that the move to a pluralist approach to fitness measurement led to questions as to what fundamentally unites the various fitness metrics we had examined and what distinguishes valid from invalid metrics. It stands to reason that the various metrics we have looked at so far – those which are typically discussed in the literature – are not simply plucked from thin air. They *do* have something in common and we could *not* just pick any old quantity to serve as a fitness measure. It is ultimately the lack of an underlying fitness concept that prevents us from being able to explicitly state this unifying characteristic. Here, I contest that a thermodynamic approach lets us answer these questions.

In chapter four, Van Valen seemed to get at something close to the truth with his attempt to use energy as a common currency, unifying the disparate aspects of fitness. Energy consumption turned out to be a fatally flawed metric, though, as was the wider idea of using an "input" to track fitness as an "output". However, there still appears to be room for progress by retaining a "physicist's eye view" of selection, looking for other metrics and confining consideration to the "output side".

1.1. Back to Basics

We begin by going back to basics to ask what reproduction, persistence and growth have in common. As seen in chapter two, the conceptual boundary between reproduction and growth is an ambiguous one. Reproduction might be conceptually distinguished from growth as involving the creation of physically discrete units or by the more sophisticated criterion of requiring a single-cell bottleneck to re-start development (Godfrey-Smith 2009, Dawkins 1976). However, examples like that of the quaking aspen, show that the two phenomena can be difficult to distinguish empirically (chapter two, section 2.1); even via the former, relatively simple criterion. Theorists also often make valuable insights by blurring the lines between growth and reproduction. For instance, Janzen (1977) makes enlightening points on the adaptive strategies of aphids and dandelions by discussing their reproduction in terms of the growth of a single, large, spatially distributed organism.

In simple terms, reproduction and growth seem alike in that both involve an entity "making more of itself", with distinctions made between the two concepts according to the specifics of how this occurs. We might think, then, that fitness is something to do with this business of "making more". However, even under a standard, numerosity approach, persistence alone can contribute to fitness (as explained in chapter two). Thus, we can recognise the survival, or even relatively slow decline, of a type within a population as corresponding to elevated fitness in appropriate circumstances. Persistence, though, does not obviously involve making more of anything, so much as preserving what is already there, so this idea of "making more" will not suffice.

1.2. Thermodynamic Definition of Life

So, we have the idea that fitness is something to do with an entity making more of itself and/or maintaining what is already there over time. We can also add the idea from the previous chapter that fitness-related processes are accomplished via the input of energy or resources. All this might seem rather familiar to those acquainted with the definition of life literature as seeming closely related to the thermodynamic definition of life – perhaps the single leading approach to defining life currently. In non-technical terms (which I will make more precise presently), this definition sees a living being as a system that maintains or builds upon its own ordered structure by means of disordering its surroundings.

This approach to defining life is often summarised as seeing life forms as "local inversions" of the second law of thermodynamics (Schrödinger 1944, Weber 2018). The second law can be defined in multiple ways, but generally leads us to expect the entropy in a closed system – and thus across the universe as a whole – to increase over time. As a result, the universe moves inexorably towards "heat death", where entropy is maximised. Entropy is often translated into lay terms as quantifying the "disorder" of a system. This is actually something of a false equivalence, and can be misleading in some contexts (Corning and Kline 1998), but will be a useful approximation for our purposes. In that frame, then, we can think of the second law as an expectation that disorder will increase over time, with ordered structures inevitably facing decay.

Much of the material world seems to very straightforwardly abide by the second law. We see it in action when cliff faces are degraded rather than built up by the sea, stones roll down rather than crawl up hills and sugar lumps dissolve and do not reform in hot cups of coffee. In all such cases, we observe a move from low to high entropy at the local level. However, life does not seem to play along. Instead, we see lifeforms as highly ordered structures, not degrading over time, but persisting and even increasing in the amount of order they, and any offspring they produce, embody – that is, maintaining or even lowering their entropy.

Since the second law forbids any net decrease in entropy, this initial impression can lead to life appearing somewhat mysterious and has helped drive historical ideas that there was something "special" about life that could not be accounted for by the standard laws of physics. In this vein, Lotka comments:

> The principle of natural selection reveals itself as capable of yielding information which the first and second laws of thermodynamics are not competent to furnish (Lotka 1922:151)

However, in his book *What is Life* (1944), Schrödinger proposed that the apparent "entropy debt" (to use his term) accrued by living beings is paid off by generating an equal or greater degree of entropy in their surroundings. Thus, life is able to conduct its characteristic behaviours without breaching the second law, via a constant throughput of order (in the form of either ordered material or energy) from the environment, which is made use of before being expelled in a disordered form. Thus, Schrödinger states that:

> The device by which an organism maintains itself stationary at a fairly high level of orderliness (= fairly low level of entropy) really consists in continually sucking orderliness from its environment (Schrödinger 1944:75).

Of course, in less abstract terms, this is precisely what we observe when we see organisms maintain themselves, and thus their metabolisms, by ingesting food or absorbing sunlight for photosynthesis[11] and subsequently excreting material waste and heat energy. This imbibed order is more technically thought of as "negative entropy" in Schrödinger's terminology, with the term "negentropy", which I will use interchangeably here, later applied by Brillouin (1949). Thus, Schrödinger states that an organism "can only keep ... alive, by continually drawing from its environment negative entropy... What an organism feeds on is negative entropy" (1944:72). In later works, this flow of negentropy is more commonly reconceptualised as a flux of energy (as in Chaisson 2011 and Wicken 1980, 1986) and life is recast as a subset of the category of "dissipative structures" (Weber 2018), which emerge along energy gradients (more in section 4.4). A contemporary characterisation of life along these lines is found in the following extract from Jantsch:

> "With the help of this energy and matter exchange with the environment, the system maintains its inner non-equilibrium, and the non-equilibrium in turn maintains the exchange process… A dissipative structure continuously renews itself and maintains a particular dynamic regime, a globally stable space-time structure" (Jantsch 1980, also quoted in Weber 2018)

Disputes are possible over which characterisation is most appropriate in terms of the underlying physics (Perutz 1987), though the options are equivalent for our purposes. We retain the idea of life as a system being reliant on some flux of negentropy/material/resources/energy. The focus of our interest here is ultimately in what that system *accomplishes* by virtue of that throughput – that is, the maintenance or increase of its order/negentropy over time. This is the activity that seems to map so neatly onto the behaviour we associate with fitness. Reproduction and growth mean the creation of additional ordered material in the form of offspring or new somatic tissue respectively, whilst persistence means resisting the decay of ordered material over time predicted by the second law.

1.3. Merging Accounts

We can see, then, that the previously disparate metrics we examined in chapter two can potentially be united in contributing to this singular business of maintaining and/or expanding ordered structures against a background of general decay. In section three, I will thus begin to outline an account measuring fitness as some function of negentropy, so as to provide a common currency between the various aspects of fitness – reproduction, growth, persistence and any other candidates. In effect, then, whilst

[11] Photosynthesisers maintain and increase their own order by virtue of the energy released as order decays in the sun. Indeed, as per Bernstein et al (1983:188), we can extend this idea to note that, in its entirety, "the biosphere is an open thermodynamic system, maintained far from thermodynamic equilibrium by the constant flow of energy from the sun".

Schrödinger and others have used a thermodynamic account to qualitatively define what constitutes life, I will associate fitness with what we might take to be the "magnitude" of that life. This has the pleasing result of allowing us to make statements along the line that a relatively fit organism is a more successful lifeform.

2. Provenance

Before going further, some historical remarks will be helpful. To those unfamiliar with the relevant literature, the idea of a thermodynamic account of fitness will likely seem eccentric. However, my account should simply be taken as a fairly straightforward addition to a large, existing body of work on definitions of life and large-scale trends in evolution tackled from the same, broadly thermodynamic perspective. My treatment here simply maps this general approach to biology onto the subject of fitness and can be regarded as relatively innocuous in that regard. I also suspect some readers will be inherently sceptical of *any* thermodynamic approach to biology. Hopefully, examining the long history of such accounts will somewhat sanitise this way of thinking.

It is particularly helpful to observe that similar characterisations of life had been made in different times and places, long before Schrödinger's 1944 book (and the 1943 lectures upon which they were based). Simultaneously, Schrodinger's contribution subsequently jump-started a great deal of productive research in the same vein, which continues to the present day. These facts should provide some reassurance that this thermodynamic approach to biology is not an unreasonable one. Rather, whilst occasionally making use of rarefied terminology, a thermodynamic viewpoint really just provides us with language to express deeply intuitive facts about the phenomenon of life – and has already proved to be a productive direction for research.

Schrödinger built upon much that had gone before and his seminal book has been regarded more as a popularisation than a truly novel contribution (Perutz 1987). Indeed, Boltzmann had framed life in explicitly thermodynamic terms as early as 1886:

> Hence the general battle for existence of living organisms is not one for the basic substances – these substances are abundant in the air, in the water and on the ground – also not for energy that every body contains abundantly, though unfortunately in a non-available form, but for entropy which becomes available by the transition of energy from the hot sun to the cold earth. (Boltzmann 1886, as quoted in Perutz 1987)

Even outside explicitly thermodynamic theory, strikingly similar ideas as to the fundamental nature of life show up well before Schrödinger. Notably, in his 1927 *Outline of Philosophy*, Bertrand Russell provided a similar characterisation of life. The penultimate sentence here has become a famous quote from Russell, but the point is made even more clearly across the rest of the passage:

> Living matter, within limits, has the chemical peculiarity of being self-perpetuating, and of conferring its own chemical composition upon other matter composed of the right elements. One spore falling into a stagnant pond may produce millions of minute vegetable organisms; these, in turn, enable one small animal to myriads of descendants living on the small plants; these, in turn, provide for larger animals, newts, tadpoles, fishes, etc. In the end, there is enormously more protoplasm in that region than there was to begin with. This is no doubt explicable as a result of the chemical constitution of living matter. But this purely chemical self-preservation and collective growth is at the bottom of everything else that characterises the behaviour of living things. Every living thing is a sort of imperialist, seeking to transform as much as possible of its environment into itself and its seed... We may regard the whole of evolution as flowing from this 'chemical imperialism' of living matter. (Russell 1927:30)

Around the same time, Lotka (1922, 1944, 1945) was developing an account of life forms as systems developing so as to maximise their throughput of energy, according to his Maximum Power Principle. Lotka's principle has given rise to a tradition in its own right, directly inspiring Odum and Pinkerton (1955) and with strong echoes of his work also detectable in that of Van Valen (1973, 1975, 1976, 1979) and across the non-equilibrium thermodynamics literature, notably in Chaisson (2011) and Wicken (1980, 1986).

Schrödinger's book itself – very much the fulcrum in this tradition – has been credited with multiple different strands of influence. The picture of life it popularised helped form the intellectual background for the "replicator-interactor" theory of selection, associated with Dawkins and Hull (Dawkins 1976, Hull 1988, Bernstein et al 1983, Weber 2018). More directly, Schrödinger's account has given rise to a whole tradition in the definition of life literature, with his basic view being developed in multiple different iterations; including the "autopoietic" account associated with Maturana and Varela (1974, 1980), which has been influential in its own right. Similar ideas are often invoked in the diagnostic schemes proposed in xenobiology (as in Azua-Bustos and Vega-Martinez 2013 – discussed later). *What is Life?* also kick-started a great deal of research on the properties of the kind of thermodynamic system which Schrödinger described. In the past few decades, a substantial body of work has been amassed on the genesis and development of the "dissipative structures" referred to above.

These are only a notable subset of thinkers who can be cited as having interpreted life and evolution in a similar manner, and a much longer, more detailed examination of the pedigree of these ideas would be possible (Corning and Kline 1998 also provides a useful review). However, whilst I will return to discuss some aspects of this literature in greater detail, this chapter is not intended as a history essay. Hopefully, the point has been established that discussion of biology in thermodynamic or related terms is neither novel nor particularly esoteric and should not be viewed with undue suspicion.

3. Sketching a Thermodynamic Approach to Fitness

Going forward, then, each of the fitness metrics we have discussed in the previous two chapters can be thought of as one way in which a system can locally run counter to the second law in the manner Schrödinger described. In chapter two, I noted that we could not reduce these three metrics to any one of their number, as they failed to track one another in various situations. However, a negentropy-based measure should track each of these metrics. Increasing biomass via either growth or reproduction will imply a local increase in negentropy/decrease in entropy. Persistence will mean maintaining a certain level of negentropy over time, locally resisting the decay of ordered structure/increase in entropy which we would usually expect under the second law. In terms of any further, putative fitness metrics which we might wish to make use of, it also seems difficult to imagine any plausible metric which would not similarly track the maintenance or expansion of ordered structure.

Under this view, then, when we make use of a fitness metric like numerosity, persistence or biomass, we are making use of a proxy for negentropy which will reliably capture the action of selection in a certain subset of scenarios. Thus, numerosity tracks fitness perfectly well in many "familiar" species – where individuals generally exhibit roughly equivalent sets of properties across the board, counting individuals will robustly track total negative entropy. However, with selection involving organisms like the Washington fungus or quaking aspen, we switch to a different metric, such as biomass or persistence, to better capture biological success in that scenario. In those cases, the chosen metric better tracks the negentropy underlying fitness. To then make direct comparisons between fitness values in terms of more than one of these metrics, we should notionally be able to employ a direct measure of negentropy as a "common currency" which will capture the action of selection in *all* cases.

Thus, even where we might make use of a proxy for negative entropy, such as biomass for the aspen, we select that proxy measure for its ability to track negentropy in the scenario we are looking at. This relationship to negative entropy – and ultimately to Schrödinger's definition of life – is ultimately what renders that measure meaningful.

There is a level at which this view of fitness is an inherently comparative one. Measuring the degree to which an entity has locally defied system-wide decay will ultimately have to be done relative to a background level of decay that we would have expected over the same period of time. As such, fitness will be associated with the *extent* to which an entity departs from the behaviour of the system more generally.

Of course, fitness as a function of comparative performance is already a feature of conventional approaches to selection. A clear example is how we might consider selection in a declining population within a typical, numerosity scheme – even if all types are declining towards extinction, the type declining least rapidly is deemed fittest. Developing a thermodynamic approach to fitness would mean expanding this idea of outperforming expectation of decay to encompass all forms of selection at a fundamental level. Every lineage heads towards inevitable extinction, as all systems run down and the universe as a whole marches towards heat death. Just as we notice the presence of life by how it appears to temporarily "buck this trend", so we might appreciate fitness in terms of just *how much* an entity or lineage succeeds in this temporary defiance – enduring for longer, producing more ordered somatic tissue or more offspring during that time period.

The same theme of comparison against baseline performance will recur in the following chapter on the Darwinian population concept. For the time being, though, we risk getting ahead of ourselves with too much discussion of the details of a thermodynamic approach. Before worrying about nuance, we need to focus on foundations. Any full development of a thermodynamic theory of fitness, and of selection more generally, will rest upon a suitable fitness metric. In turn, any such metric will be a function of some measure of order or negative entropy in a biological context. Without such a workable basic measure, discussion of the finer points of elaborating a thermodynamic treatment of fitness might be rendered moot.

However, those even passingly acquainted with the relevant physics will likely already harbour significant doubts as to the prospect of any suitable negentropy measure being available. As such, my main concern with this chapter will be the possibility of deriving this kind of measure. Only after examining this issue – and thus establishing the bounds of the possible as regards a thermodynamic approach to fitness – will I return to consider my account's broader implications.

3.1. An Aside: Why Not Just Measure Biomass?

Some readers will no doubt have noted that we can also think about reproduction, growth and persistence in terms of creating or maintaining biomass. Thus, they might wonder why we cannot just measure the accrual or maintenance of biomass over time to track fitness.

Several responses are possible here, but I will focus on just a couple. First, "biomass" is not well-defined. Referring to biomass leaves us with the immediate need to then define precisely what we mean by that term. Ultimately, we will require an accompanying definition of life to tell us what counts as biomass and what does not. Ironically, if we then end up referring to the popular thermodynamic account of life to delineate biomass, we might end up pretty well back to my account. By contrast, my approach to fitness in terms of negative entropy means referring to a fundamental physical quantity and is already embedded in perhaps the most widely accepted definition of life.

Beyond this, basing a theory around biomass limits its application to living biological entities. As per the discussion in chapter four, section 3.3, limiting selection to biomass would cause severe problems in accounting for selection amongst non-metabolic, dormant or other non-living entities (prions, for example), as well as in dealing with cultural selection and indeed the origins of life and biomass itself. My own approach, as will be discussed, readily applies to such non-living and/or non-metabolic entities, avoiding such issues.

4. Deriving a Metric

A functioning, quantified metric would form the cornerstone of any fully developed thermodynamic approach to fitness. It is fairly straightforward that negentropy ought to vary along with each of the "local" fitness metrics we have considered – reproduction, growth and persistence. However, this is a rather limited conclusion. All we have established so far is that negentropy will indeed vary in *some proportion* to each fitness metric, with no detail as to the precise relationships involved – and thus still no idea of how we can objectively weigh these metrics against one another, as per our original goal. To be able to rigorously compare the fitness of entities that exhibit success in terms of different aspects of fitness, we will need a quantified "common currency" metric. Thus, to really get an idea of how the fitness of a quaking aspen that spreads by sexual reproduction of new groves compares to one that spreads by growth of a single grove, we would need to understand more precisely how reproduction and growth relate to negentropy in quantitative terms.

As discussed previously, a unifying fitness metric would confer a significant increase in explanatory scope for our theory of natural selection right away – this would be sufficient to capture selection acting between our hypothetical aspen variants above, for instance. However, since it does not invoke ideas of competition or similar, which would tie it to a specific Darwinian population, a negentropy-based metric offers the possibility of generating an *absolute* metric. In the previous chapter, I discussed benefits that might be associated with such a singular, quantitative fitness metric (promised but not delivered by Van

Valen's "advanced", energy-based account). In particular, these included a huge increase in explanatory scope for our theory of natural selection by allowing for a hugely expanded, and often radical, set of possible fitness comparisons. If realised, this would potentially drive a unifying paradigm shift in how we consider subjects like ecology and macro-level trends in evolution. For instance, as per Van Valen (1975), we might regard evolutionary transitions between trophic levels as enhancing or diminishing absolute fitness – something which would not be possible currently.

Beyond these payoffs, though, another reason to explore the possibility of a quantitative fitness metric is simply the fact that any fitness concept will find one of its primary concerns in the actual measurement of fitness in practice. As such, it would be a poor showing for me to propose taking a thermodynamic approach to fitness and not provide some commentary as to the possibility of it being developed into a fully functioning measure.

Here, I will examine two broad routes to generating a negentropy measure before using existing, related literature to rule out inviable options. Note that it would be possible to get bogged down in discussion as to the *optimal* form such a measure might take. The literature around thermodynamics pertaining to life and evolution has plenty of disagreement that might be read across to the task of deriving a fitness metric. However, I will not be concerned with debates such as to how *precisely* we ought to conceptualise order/negentropy or related concepts here. Such considerations can be set aside, as any thermodynamic measurement of fitness will depend on *some* measure of order/negentropy and the difficulty we will encounter with defining *any* such metric will rule out the luxury of considering which we might prefer.

4.1. Two Approaches

The picture of a living entity we take from Schrödinger and others is of a structure maintaining and/or proliferating, dependent upon a flux of energy, ordered material or negentropy flowing through it. Thus, we can separate two possible avenues via which we might try to derive a thermodynamic fitness metric:

1. Measure the flux of energy/resources/negentropy flowing through the system. This might be considered as significant in itself or (perhaps more likely) as a useful proxy for the negentropy instantiated in the ordered structure of the system itself.
2. Make a direct measurement of the order or negentropy of the focal system.

To put this distinction in more concrete terms, let us imagine that we are trying to measure the fitness of a reproducing organism. Thus, under the first approach, we might track the energy/resource/negentropy throughput of the initial organism and its offspring. Under the second approach, we would directly measure the negentropy instantiated in the organism and its offspring.

4.2. Dismissing Flux-Based Measures

Readers will have noticed that the first approach above sounds much like the “consumption” accounts of fitness we examined in the last chapter. Indeed, we can immediately rule out this first approach to measuring the negentropy of a system based on the points made there. Regardless of any interpretation in terms of negentropy, chapter four has already demonstrated the existence of various efficiency problems, such that the input into a biological system in terms of resources, energy or similar is a poor proxy for fitness-relevant outputs. Thus, we cannot expect flux-based measurements to reliably track fitness and can eliminate the first option.

4.3. Direct Measurement of Negentropy

Our remaining candidate is thus the second approach above – a more direct assessment of the negentropy/order associated with fitness. This allows us to avoid the efficiency concerns accompanying any measure of output via input. Additionally, whilst I will focus here on metabolic or "living" entities – systems with an energy/negentropy flow through them – a direct measure of negentropy should apply just as readily to a non-metabolic/non-living system (discussed in section 6.2). As noted, a thermodynamic account does not inherently require any recourse to competition or similar notions and so does not run into problems in that regard. Already, then, we are avoiding the major problems with Van Valen’s work and consumption accounts in general

4.4. Existing Measures

Unfortunately, there is no convenient, existing account in the literature for us to refer to here, as Van Valen provides for flux-based metrics. However, whilst there is no pre-existing, explicit account of fitness in terms of order, negentropy or similar, there has been a good deal of work on thermodynamic approaches to life and evolution more generally – with some explicit measures of entropy and related quantities. These are deployed within contexts other than fitness measurement but seem ostensibly relevant to our purposes.

As alluded to above, as well as giving rise to a prominent school of thought in the definition of life literature, Schrödinger's work sits at the beginning of a whole body of research studying the characteristics of the kind of self-ordering systems he described in *What is Life*. Since that book, a significant volume of work on the subject has been produced across several related fields; including biophysics, non-equilibrium thermodynamics and theoretical ecology.

As noted, a general world view has emerged between the various authors in this area (Sneider and Kay 1995, Weber 2018). This sees self-organising behaviour as the inevitable result of applying an energy gradient across a system. Such a gradient will initially function to displace the system away from

equilibrium. However, the system will respond with the emergence of structures acting to dissipate that energy gradient and resist further movement away from equilibrium. The expectation is that these "dissipative structures" will develop so as to maximise the rate at which they throughput energy; possibly maximising their own structural complexity as they do so. As well as working within the legacy of Schrödinger's thermodynamic approach, work like that of Chaisson (2011) and Wicken (1980, 1986) shows strong convergence on Lotka (1922, 1944, 1945) and successors' (such as Odum and Pinkerton, 1955) writings on the Maximum Power Principle.

A number of quantitative measures of negentropy and related quantities have emerged from this wider body of work. Importantly, though, authors have been concerned with the development of ecosystems and directional trends in evolution, rather than with the derivation of fitness metrics. As a result, they have generally attempted to measure negentropy as an *intensive*, rather than *extensive*, property[12]; measuring complexity as something like the "density" of negentropy, as opposed to its magnitude. In simpler terms, we might say that the measures they have developed quantify the degree of complexity of the systems they are applied to, rather than the amount of order which they contain. To employ the similar distinction from Sneider and Kay (1995), the authors working in this area have been interested in the "development" of systems, rather than their "growth". Sneider and Key explain the difference between these concepts as follows:

> "Biologic growth occurs when the system adds more of the same types of pathways for degrading imposed gradients. Biologic development occurs when new types of pathways for degrading imposed gradients emerge in the system." (Sneider and Kay 1995)

It is with this same focus on complexity that Chaisson (2011) puts forward his "energy rate density" measure. This records the energy flux through a system per unit time, per unit mass of that system as a proxy for the system's complexity. Crucially, though, energy rate density is clearly an intensive, rather than extensive measure, by virtue of its being scaled per unit mass. Thus, if we doubled the physical size of the target system, whilst keeping the same level of structural complexity – for example, by doubling the number of individuals of some homogenous type – the energy rate density would retain the same value, as the energy flux per kilo of mass would remain the same. Chaisson often gives the human brain as an example of one of the highest energy rate densities in the known universe. The energy rate density of a human brain, then, would be higher than that of the much more physically massive, but less complex, brain of a sperm whale (possessed of the largest brain in nature, as per Kojima 1951

[12] As will be discussed, in physics, the same term "entropy" is confusingly used to refer to two distinct quantities – one intensive and one extensive.

and Burger et al 2019), even though the latter would clearly represent a greater volume of ordered material/total negentropy.

Astrobiologists Azua-Bustos and Vega-Marinez (2013) operate in the same broad theoretical framework but make use of rather different methods. The pair propose using fractal complexity analysis to detect unfamiliar forms of life via a measure of their entropy. Their rationale begins from this same fundamental picture of life, with living beings maintaining their own order/low entropy/high negentropy by exporting disorder/entropy to their environment. Thus, they reason that life anywhere in the universe can be expected to manifest a greater degree of structural complexity than that of its abiotic surroundings. Searching out this differential in complexity is then suggested as a diagnostic criterion for distinguishing life from non-life, which can be applied regardless of the specific material constitution of the putative life form.

As mathematically complex as their terminology might sound, Azua-Bustos and Vega-Marinez's high-level explanation of their method is qualitatively quite simple. Filtered photographs of putative organisms and their abiotic surroundings are compared – in one trial, bare rock is compared with surfaces colonised with lichen. The pair's fractal analysis tool then provides a quantification of the spatial scale at which the structures of each are arranged. One can think of this as how far one has to "zoom in" to perceive the "grain" of the relevant structures. A significant differential, such that the target is arranged on a much smaller scale than its surroundings, is taken as evidence that the more complex formation has been generated as part of a life form. This metric is explicitly intended by Azua-Bustos and Vega-Marinez as a measure of relative entropy, with life forms expected to have lower entropy (that is, higher negentropy) than their surroundings. Indeed, their approach is a pleasing material analogue to the rationale by which SETI radio-telescopes search for ordered artificial signals suggestive of intelligent life amongst the interstellar noise.

In much the same manner as Chaisson's energy rate density, this is an intensive rather than extensive measure. The lichen Azua-Bustos and Vega-Marinez studied might spread over double or triple the area of rock, but their method will continue to ascribe it the same value of entropy as before. Only the complexity of the structure is measured, not its size – and I will demonstrate that this is not suitable for a fitness metric.

4.5. Rejecting Existing Measures

It might be tempting to try to employ these intensive measures as the basis for a fitness metric. After all, we might reason, if evolution proceeds in a way that increases these quantities over time, then we should be able to assess fitness via those quantities. We might think that these "complexity" measures

of the degree or density of negentropy might act to measure fitness, on grounds that we would expect evolution to bring forward forms with ever greater complexity/degree of negentropy.

However, we can rule out the idea that fitness can be measured as a function of complexity immediately. We can do so for two reasons, which I will examine in turn.

4.5.1. We Require an Extensive, Rather Than Intensive, Measure

There is significant scope for confusion around language, which might lead us into error. Specifically, the term entropy, and thus the term negentropy, can be taken to refer to both intensive and extensive quantities, depending on the context. Thus, in physics and elsewhere, the same words "entropy" and "negentropy" can correctly refer both to the *amount* of, respectively, disorder or order a system (the extensive sense) and to the complexity of that system – something like the *degree* or even *density* of order (the intensive sense). Thus, when we read authors like Chaisson (2011) discussing metrics devised to measure the entropy of systems, it sounds like we might be able to use those measurements as the basis for a fitness metric.

However, fitness, as we have been considering it throughout our analysis, is fundamentally not a matter of intensity, but one of extent – and is thus measured by *extensive* metrics. When an organism produces offspring, grows new somatic tissue or maintains itself over an extended period of time, that organism is creating or preserving material of the *same* degree of complexity. When a rabbit does as rabbits are wont to do and contributes to its fitness by producing numerous offspring, there is an increase in the number of individuals with the same structure. This is an increase in total order without any meaningful increase in complexity. By the same token, when the Washington Fungus (discussed in chapter two) grows larger or lives longer, it does not become significantly more complex, but simply increases the volume of material with the same structural complexity or the length of time that material persists for.

By contrast, and as we have already noted, the complexity metrics put forward in the non-equilibrium thermodynamics tradition will not record this kind of increase in the physical or temporal extent of the target system. Under Chaisson's or Azua-Bustos and Vega-Marinez metrics, the biomass of an individual or lineage could increase one hundredfold via reproduction or growth – a massive increase in realised fitness by whichever standard – without this leading to any change in the measured complexity of the system. Thus, despite linguistic confusion, the existing thermodynamic measures of the biological world are simply of a completely different character to what we require as the basis for a fitness metric.

4.5.2. Large Scale Trends in Evolution Are Not Relevant to Fitness

Intensive measures of negentropy and related quantities are used by Chaisson, Wicken and others to track apparent trends in the direction of evolution. It would be tempting to imagine that such measures might be relevant to the assessment of fitness. After all, what else is fitness measurement, and selective theory more generally, if not a tool to explain the course taken by evolutionary change?

Ideas of directionality and/or large-scale trends in evolution are not new and are not confined to a thermodynamic world view (McShea 1998). Various putative trends, such as directional changes in body size, have been put forward[13]. However, these large-scale trends in evolution are generally separated from matters of fitness and immediate-level selection. For example, even if we are convinced that evolution tends to increase body size over time, we do not then automatically suppose that larger organisms will necessarily be fitter. We can also think about the relationship the other way around. Thus, with a conventional numerosity account of fitness, we would expect selection to favour variants producing greater numbers of offspring or gene copies, but do not expect the absolute fecundity of forms to increase over time, with species producing ever greater numbers of offspring as they evolve. Indeed, Lack (1947) on clutch sizes and the literature on K-selection (Pianka 1970) shows that there are circumstances where we should expect selection to favour variants producing lower numbers of offspring.

It might seem odd that "macro" scale trends in evolution are not relevant to the "micro" level of selection. To understand why, we can think about the large-scale trends proposed for evolutionary change as statistical laws. When such laws specify the direction of global, system-wide trends, they do not necessitate that every part of the relevant system will proceed in the stated direction at all times – only that the system will do so in aggregate over sufficiently long periods of time. Perhaps the best example of such a law is one we have already been dealing with. The second law of thermodynamics dictates that any closed system will proceed to increase its entropy over time. However, the characteristic behaviour associated with life occurs precisely whenever subsets of the total, closed system do *not* proceed in the same direction as the system as a whole. It would be absurd to recognise this, but then expect each individual living being to abide locally by another global statistical law. Thus, we cannot expect that selection will always favour increased complexity just because we expect that evolution will proceed in that direction generally. As such, we cannot sensibly use measures of negentropy as an intensive quantity as the basis for a fitness measurement.

[13] Indeed, Demetrius (2000) might be seen as wedding traditions by arguing for trends in body size and longevity as a result of thermodynamic considerations.

5. Prospects for a Useful Measure of Negative Entropy

By now, we have thoroughly established that we cannot extract a suitable, extensive measure of negentropy from the existing literature. As such, if we want such a measurement, we will have to come up with it ourselves. However, it will become apparent that one of the reasons such a measure is not already available "off the shelf" is likely because of the inherent, and likely insurmountable, difficulties associated with deriving one. To give a full explanation as to the nature and magnitude of these problems, it is necessary to take a brief detour to examine the idea of entropy in a little more detail. In doing so, we will discover serious problems with a negentropy measure both in principle and in terms of the practicalities of ever hoping to apply such a measure.

5.1. Difficulties in Principle

The difficulty in quantifying entropy – and thus negative entropy – in absolute terms mean that scientists will usually concern themselves with the magnitude and direction of changes in either rather than absolute start or end values. In physics, there are indeed cases where it is possible to ascribe absolute entropy values. However, this can only be accomplished in the instance of a pure substance existing as a crystal at zero degrees Kelvin (Lewis and Randall 1923). In this state, the system will have zero entropy. We can then estimate the increase in entropy associated with incrementally raising the system's temperature.

Obviously, this kind of special case is not terribly relevant to us in driving a fitness measure. After all, there are few situations where we might want to quantify the fitness of a crystal. The fundamental barrier to being able to assign absolute measures of entropy and negentropy more widely is the fact that, in order to do so, we must be able to enumerate all possible states of the relevant system. In short, this is because entropy (and thus negentropy) is defined as a function of the number of possible microstates of a system that can manifest the same observed macrostate.

Specifying all the states of a system will mean enumerating all the possible configurations which we might find the relevant matter in at a microscopic level, given what we can observe of that system's overall, external appearance. The crucial problem is that these configurations might differ from one another in terms of *continuous* quantities. A pure crystalline substance at zero degrees Kelvin has only one possible microstate, as the relative positions and distances between each atom are all fixed within the crystal's structure. In the example of a pure, monocrystalline diamond at absolute zero, we know that the characteristic repeating tetrahedral structure means there is only one possible configuration of carbon atoms giving rise to a crystal of the observed dimensions.

However, if we consider a liquid or gas, where atoms can flow, moving around relative to one another, we introduce this possibility that states might differ from one another in terms of continuous variables, including spatial position. In a crystal, the distance between atoms is fixed. In a gas or liquid, though, distances might take an infinite number of values. The number of possible microstates corresponding to any macrostate will thus also be infinite. In principle, this yields an infinite value for entropy in all cases – useless for any comparative purposes and generally considered simply undefined in practice.

Some branches of physics do deal in what are put forward as non-infinite absolute entropy values, suitable for comparison. However, these will all rely on imposing some kind of granular partitioning of space – generally around the Planck length – transforming distance from a continuous to a discrete quantity (as per Ehrenfest 1911 on what is known as “coarse-graining”; discussed in Wehrl 1991 and Gorban 2006). Whether such discrete treatment of space is representative of physical reality is still a matter of discussion. Often, space will be handled in this manner as an explicitly artificial way of generating absolute entropy values. However, some variants of physical theory envision space as a discrete, quantised phenomenon. As a third approach, some theories place a "perceptual limit" around the Planck length (Wehrl 1991:120), reasoning that we will not be able to discern states of systems that differ in such minuscule terms, and thus judging these differences as irrelevant to the calculation of entropy values.

Whether useful absolute entropy values can ever be more than a pragmatic artifice is still very much an open question in physics. As such, whilst the prospects are not particularly rosy, we cannot yet know for certain whether absolute measures of negentropy could ever be applied to the natural world – and thus whether such a measure might eventually form the basis of a quantified, absolute, thermodynamic fitness metric.

5.2. Difficulties in Practice

Pragmatically, whether absolute measures of negentropy might be available in principle is something of a moot point, as such measures could never hope to be applied to real cases. Even if space turned out to be discrete rather than continuous, the task of enumerating all possible states, even for a system of just a few atoms, would be computationally daunting. For anything as large and complex as a life form, calculations rapidly become totally intractable. In practice then, regardless of fundamental physics, we will always be confined to making use of local proxies to assess negentropy.

6. Implications

These problems across both principle and practice conclusively rule out ever deriving a working, *extensive* measure of negentropy in the biological sphere. Without this basis, we cannot hope to assemble a quantitative, singular, "common currency" fitness metric as I have discussed it. The immediate implications of this fact might seem fairly damning for my approach in general. However, even in the absence of a direct metric, a thermodynamic approach to fitness still has a lot to recommend it, especially at the conceptual level.

6.1. Immediate Implications

With no direct measurement of negentropy, we will not be able to derive a singular, thermodynamic fitness metric by which to quantitatively reconcile the various disparate aspects of fitness we have discussed. Thus, in terms of the immediate business of fitness measurement, we are forced to fall back to the metric-pluralist scheme arrived at in chapter two. Of course, as I spelt out in chapter two, the metric pluralist stance already enjoys significant advantages over any conventional, monist account – so we are still well "up" on our starting position. However, no "common currency" metric means that we will not be able to rigorously compare fitness values manifested across different dimensions of biological success.

For example, we might return to a previous hypothetical (from chapter two, section 3.2.1) comparing the fitness of purely sexually reproductive and purely asexual variants of quaking aspen. If one variant produces offspring groves and one simply grows very large as a single grove, we will not be able to say with any absolute certainty which variant has been the more successful, as to do so would require a common currency between biomass and numerosity. Of course, if we have no metric at all, that metric cannot be an absolute one, and so we also lose out on the ability to make any of the more "radical" fitness comparisons of the kind promised by Van Valen's "advanced" account.

6.2. Wider Implications

If we simply stopped at this point, we would take away a fairly negative appraisal of the thermodynamic approach I have proposed. However, we are in a rather better position than might initially appear. Whilst this approach cannot offer us a working fitness metric, it can still offer significant gains at the conceptual level.

Thus, we might not have a "common currency" metric to unify the various aspects of fitness, but the thermodynamic approach still promises to unite reproduction, growth, persistence and any other candidate metrics conceptually, granting them meaning by relating them back to Schrödinger's

definition of life. This does a lot to underpin and de-mystify a metric-pluralist approach to measurement. Indeed, a thermodynamic interpretation of fitness offers rather more in this regard than many more mainstream accounts, which simply make vague gestures at some underlying phenomenon of fitness without ever really cashing this out (as in Williams 1970, for example).

So, we answer the question posed at the end of chapter two as to what the various metrics we might employ have in common: tracking negative entropy. We will also be in a position to make a principled assessment as to the validity of any proposed additional metrics to be added alongside numerosity, biomass and persistence by assessing whether they usefully track negative entropy in some subset of scenarios. As an example, we have already seen that we can explain why consumption metrics like those provided by Van Valen might track fitness in some cases – perhaps when efficiency issues happen to be minimal or particularly where we are directly concerned with competitive ability in resource capture. However, we can also understand why these metrics fail to capture selective reality in non-metabolic cases; such as that of selection amongst seeds or prions, considered in chapter four, section 3.3. Seeds and prions, as ordered structures, will instantiate negentropy without any flux of energy or resources channelled through them. Without that flow, though, consumption-based metrics will fail to track that negentropy and thus fail to capture selection.

When we then chose to make use of some other metric (perhaps persistence-based) in considering fitness amongst seeds, we can warrant this within a wider conceptual framework. Thus, with a thermodynamic account, we are able to refer back to the idea of tracking negentropy as the reason for alternating metrics, rather than simply citing more vague ideas like "research interests" or similar, as would have been the case previously.

More immediately relevant, perhaps, is that a thermodynamic approach to fitness better allows us to explain and understand adaptive trade-offs between different aspects of fitness made across different species. Thus, when we read Harper (1977:647-650) on the trade-offs between growth and reproduction in various plant species, we are able to rest his descriptions on a more robust footing than he provides himself. Accordingly, we will be able to explain that a variety of plant which has, for example, adapted to prioritise somatic growth over reproduction has elevated overall negentropy in doing so, even if we are not able to express that insight quantitatively.

Indeed, even without an absolute, singular fitness metric, we do not necessarily miss out on being able to make at least a subset of the radical inter-species fitness comparisons promised by Van Valen. More generally, a thermodynamic view at least provides a useful framework for *discussion* of these kinds of issues, even without allowing for definitive pronouncements.

Returning to a previous example, it seemed intuitively obvious that the common rat exhibits greater biological success than the giant panda. In this case, the differential is so stark that merely having an absolute concept of fitness in place is sufficient to warrant the idea that one is fitter than the other, even without having a quantitative metric to employ in practice. Just as we can say that a skyscraper is taller than a bungalow without needing a tape measure, even if we cannot conduct the raw computations required to calculate exact absolute fitness values for rats and pandas, we can already be sure that the common rat would be the fitter if we could indeed do the mathematics. This is a definite advance on how we consider the same case under a conventional approach – where the question of whether the panda or rat is more successful is simply not a coherent one to ask.

Of course, such clear-cut comparisons will be rare. For a comparison like Van Valen's (1975) of a human and a palm, we would require a functioning absolute fitness metric to make any definitive pronouncements. That said, the real gain is in having a conceptual framework within which to consider these issues at all. This alone promises to increase our depth of understanding of selection.

Happily, this state of affairs also happens to very neatly capture our strong intuitions (as set out in chapter four, section 2.2) concerning such comparisons. Thus, it seems very plausible, and fairly innocuous, to say that the common rat is more successful than the giant panda – to the extent that it represents a merit that an account of fitness should allow for this statement to be made. However, claims like those concerning the relative success of humans and palm trees seem intuitively very dubious and likely intractable – we do not necessarily want to embark down that road. A thermodynamic account seems to somewhat confirm and explain these intuitions and allows us to warrant the more plausible statements without also being tied to more dubious ones.

So far, then, we have accounted for much of our shopping list at the start of this chapter. Restating that list, I held that, for my account to be successful, it should grant:

- A common currency metric to render the different fitness metrics of chapter two commensurable.
- That this metric is quantitative and readily measured – as was resource or energy consumption.
- A conceptual underpinning to make sense of the multi-faceted nature of fitness observed in chapter two.
- That this conceptual underpinning not be reliant upon reference to competition.
- That we avoid efficiency problems by assessing fitness via "output" rather than "input".
- The possibility of selection in non-metabolic systems.

- Ideally, an increase the explanatory scope of our theory of natural selection by allowing for more permissive comparisons of fitness than are currently workable.

Despite not having arrived at a quantitative measure for negentropy, and so failed to provide a working common currency metric, we have still managed to conceptually unite our initially disparate fitness metrics and, in doing so, have able to salvage at least some portion of the explanatory capacity of Van Valen's work. We have also done all of this in the context of an account that avoids efficiency problems by focusing on output rather than input, without recourse to competition and whilst being able to account for selection in non-metabolic/non-living entities. Finally, we have shown that some non-standard fitness comparisons are warranted and that we have a framework to discuss such comparisons in general.

However, the thermodynamic account also offers payoffs beyond those initially sought. In particular, the single major advantage accompanying a thermodynamic account of fitness is the opportunity to unify our concepts of fitness and life. By identifying fitness as something like the magnitude of the characteristic behaviour taken as definitive of life by Schrödinger and others, we arrive at the satisfying position of being able to claim – as noted – that a relatively fit organism is a more successful lifeform.

Relatedly, a thermodynamic view also presents promising avenues for future research. In chapter two (section 4.3), we saw how a metric-pluralist stance will help to address selection acting within unconventional substrates or levels of organisation; such as cultural or clade selection. A proper conceptual underpinning for that metric pluralism will only facilitate such work. More broadly, a direct application of a thermodynamic approach to the biological world to issues around fitness and selection would break new ground, but also comes with an extensive body of literature to productively draw upon from the definition of life and non-equilibrium thermodynamics traditions. There is not sufficient space here for a great deal of additional development, but the theme of selection seen as relative to the behaviour of a wider, background system will recur in the upcoming chapter on the Darwinian population concept.

Conclusion

In this chapter, I sketched a unifying account of fitness, working from a thermodynamic view of the biological world. Fitness was seen as a reflection of the extent to which an entity succeeds in maintaining or increasing ordered structure (negentropy) against the universal decay predicted by the second law of thermodynamics – in line with Schrödinger's well-known thermodynamic definition of

life. Thus, if Schrödinger defines what it is for an entity to be alive, my account regards fitness as something like the "magnitude" of that life.

I have shown that it will not be possible to make direct use of a thermodynamic fitness metric as a quantifiable common currency between the different aspects of fitness from chapter two. This denies us the full increase in explanatory power promised in Van Valen's work, as discussed in chapter four.

However, even without offering a quantitative metric, by providing a robust conceptual underpinning for our understanding of fitness, a thermodynamic approach still allows us to achieve many of our "shopping list" of aims from the start of this chapter, retaining at least a fraction of the advantages of Van Valen's approach, whilst avoiding its major pitfalls. Beyond these initial goals, though, a very major additional payoff associated with my approach is that we are able to unite our concepts of life and biological fitness. As such, we arrive at the intuitively satisfying position of being able to say that a relatively fit organism is a more successful lifeform. To be able to do this whilst also being able to capture selection amongst non-living entities is a particularly positive outcome.

Fully developing all the details and implications of a thermodynamic approach to selection would require more than one thesis's worth of space in itself and, as such, I will largely have to defer this task. However, aspects of the upcoming chapter on the Darwinian population readily mesh with the picture I have presented here and thus indicate one promising direction in which a thermodynamic approach might be developed.

VI

DARWINIAN POPULATIONS

Of the four typical assumptions around natural selection set out in the introduction to this piece, I have now addressed three. The remaining assumption for scrutiny is that the population involved in a case of natural selection is self-evident. As such, this chapter addresses this final assumption, looking at the complications around defining the Darwinian population concept[14].

Importantly, though, this chapter is also necessary to buttress the arguments I have made up to this point. Readers might have been slightly perplexed where I have previously made points or discussed possibilities that contradict their own instincts as to how Darwinian populations ought to be defined. More crucially, though, much of the discussion in the previous chapters would be completely undercut by universal application of a conflicting Darwinian population concept.

This is most clear in the case of my claim from chapter one, that selection can proceed in the absence of competition. If we believed that competition was fundamentally necessary to have a Darwinian population, and thus to recognise selection at all, then this would render my whole argument in that chapter invalid – simply ruling out non-competitive selection as a matter of definition.

Similarly, there was a good deal of discussion of selection between members of different species across chapters four and five. This might well have raised eyebrows for readers who think of Darwinian populations as inherently drawn from a single species. Importantly, this discussion would also be rendered moot by blanket application of a Darwinian population concept mandating entities under selection together be conspecifics.

Even the move away from a strict numerosity account of fitness, as per chapter two, would subtly clash with some Darwinian population concepts. If selection is not exclusively concerned with reproduction

[14] Explicit discussion in this area has been so scarce that terminology is still not quite standardised. The simple term "population" seems too readily conflated with other groupings. As such, in this chapter, as throughout this piece, I follow Godfrey-Smith (2009) in referring to the set of entities participating in an instance of selection together as a “Darwinian population”.

and might also manifest in terms of longevity and somatic growth, this might run into problems with Darwinian populations based exclusively around reproductive relations between members.

Of course, as noted much earlier, the fundamental elements of a theoretical framework will all depend upon one another, such that destabilising one will also destabilise the others. This means that, as well as examining the last of our four assumptions, I was always going to have to do some work to analyse the Darwinian population concept and show that my points from earlier chapters are not undermined by considerations around it.

Indeed, being undermined in terms of how the Darwinian population is defined is a particularly difficult possibility to guard against, as there is no single, explicit, received account of that concept to refer to, as we had in previous chapters. Certainly, there are a multiplicity of vague ideas for criteria, such as those mentioned already, but very little in the way of stated definitions. Thus, before worrying about whether some robustly applied universal Darwinian population concept might challenge my ideas in other chapters, we first need to do the foundational work of checking whether such a concept could be made coherent at all. Happily, an analysis of our ideas around the Darwinian population is already the primary aim of this chapter. Only if some singular, coherent account were available would it then pose problems for my arguments earlier in this piece.

The acute lack of discussion of the Darwinian population concept is particularly surprising given its crucial importance for our theory of natural selection. Millstein (2009) points out that the Darwinian population concept is more fundamental than the species concept, particularly because how we define the Darwinian population can impact the inferences we draw about instances of selection. This is not simply a matter of abstract principle, but a real-world problem for empirical investigations. Wells and Richmond (1995) note a multitude of different ways in which Darwinian populations have been defined by working biologists, whilst Millstein (2009:268) demonstrates the confusion this has caused in the empirical literature. Despite this, little has been written on the Darwinian population concept – especially compared to the sprawling literature on species (Stegenga 2016, Millstein 2009).

Most of us who have not considered the issue in any depth will probably begin from something like Futuyma's textbook definitions of a "biological population". For instance:

> …a group of conspecific organisms that occupy a more or less well-defined geographic region and exhibit reproductive continuity from generation to generation (Futuyma 1986:554, referred to in Stegenga 2016).

Or similarly, the later:

> …a group of individuals of the same species which occupy a specified geographic space and may interact with one another (Futuyma 2013:12)

Each of these definitions include several of the criteria we will be examining. That this is the case is perhaps understandable, as these definitions describe fairly "run of the mill" Darwinian populations, as found in many empirical studies and, more broadly, groupings that we are accustomed to casually observing in nature. For instance, in the stock case study of industrial melanism in peppered moths (Kettlewell 1955), we see a group of conspecifics – with a reproductive causal linkage by virtue of being in a sexually reproducing species – inhabiting a shared environment/geographic location. Such a population will satisfy pretty well any of the different criteria we will be looking at. In many real biological scenarios, then, multiple putative criteria for bounding the selective set will coincide (Godfrey-Smith would regard these as "paradigm" Darwinian populations). However, as we will see, not all cases of selection manifest all these various criteria simultaneously. Some systematic analysis is required to see which criteria, if any, are universal or even meaningful.

Of the literature which does address the Darwinian population concept directly, Godfrey-Smith (2009, 2014) provides the most well-known contribution. More recently, Stegenga (2016) gives an innovative account backed by particularly thorough analysis – to which my own discussion will owe a good deal. Though authors differ on how defining the Darwinian population might be achieved, the goal of conventional accounts is something like the delineation of groupings of individuals causally linked to one another in a manner relevant to the outcomes of the particular instance of selection. Certainly, this idea of causal linkage between members of the Darwinian population seems to capture the underlying intention of authors like Futuyma who define Darwinian populations without justification of the particular method they chose.

In this chapter, I will make a systematic survey of the main contenders for criteria to bound Darwinian populations, with most referring to some causal connection between individuals under selection together. In order to add structure, I will impose a rough tripartite division[15] between criteria referring to "direct" and "indirect" causal interactions as well as non-causal criteria. I find that no conventional account will be able to function across all cases of selection – thus saving my points in the rest of this

[15] As will be discussed, it will not always be clear which category a certain criterion ought to fit into. However, this will not be problematic for my analysis – especially given the severe problems encountered by *all* of the criteria I examine.

piece from being fatally undermined. I will also suggest that one reason for confusion in defining a Darwinian population stems from our tendency to mistakenly consider some pragmatic groupings made for comparative inferences as causally bound Darwinian populations.

Schematically, discussion will be structured as follows:

1. Direct Causal Connections

I examine the potential to define Darwinian populations based on competition, cooperation or exploitation – the interactions associated with my category of strategic selection. I also examine reproduction and reproductive competition as criteria. However, clear cases of parametric selection amongst asexual organisms render any approach based on direct causal interactions unworkable.

2. Indirect Causal Connections

With direct causal connections ruled out, I consider bounding Darwinian populations via indirect causal relations. Thus, I examine defining populations by inhabiting a shared environment and by shared ancestry. However, I again find these criteria to be dysfunctional in various clear cases of selection.

3. Other Factors

To be fully thorough, I examine other factors which are often cited as definitive of the Darwinian population and which can be interpreted non-causally. Specifically, I examine the possibility of species membership and similarity as bounding Darwinian populations. I note that, despite our strong intuitions that individuals ought to be similar to be considered as undergoing selection together, selection cannot proceed without some degree of difference.

4. Findings

With no universal criterion for uniting Darwinian populations available, I conclude that a pluralist scheme as per Stegenga is the only way to proceed in grouping entities under selection. This result also renders my points in previous chapters safe from negation by a conflicting Darwinian population concept.

5. Comparison and the Darwinian Population

I consider why the Darwinian population concept proves so resistant to analysis and why we hold conflicting intuitions around it. Thus, I begin from the typical end use of the Darwinian population as a tool for making inferences and work backwards from that point. I argue that we

often group organisms pragmatically for the purposes of comparative inference as to the action of selection and that confusion emerges where we then mistake those “comparative populations” for causally bound Darwinian populations.

6. Directions for Development

I briefly indicate two particularly promising avenues for development of this idea. Thus, I note the potential for synthesis for work from Bouchard and Rosenberg and Huneman and with my own thermodynamic approach from the previous chapter.

My concluding remarks in this chapter lead into those for the thesis as a whole.

1. Direct Causal Connections

For many cases of selection, we are able to pick out a set of individuals bound together by strong, easily discerned causal interactions. Such groupings are perhaps most obvious and well-recorded in cases of competitive selection, where we readily bound groups of competitors contesting pools of resources or mates. These kinds of interactions would provide the clearest, and thus most desirable, means of defining a Darwinian population. As such, I begin with a discussion of possible means of grouping individuals under selection via such unambiguous, direct causal links.

1.1. Competition/Cooperation/Exploitation

As examined in chapter one, there is a common assumption that selection is necessarily driven by competition between those individuals involved. Ostensibly, then, we should be able to define a Darwinian population simply as all the individuals involved in the relevant competition. Indeed, Van Valen's (1973, discussed in chapter four) account of selection does precisely this. His work demonstrates that Darwinian populations can be clearly delineated relative to the specific pool of resources they compete for. As an example, we could readily identify all the trees striving for light against one another in a patch of forest as a competitively defined Darwinian population.

However, I noted in chapter one that competition was far from a universal feature of natural selection. I described cooperation and exploitation as alternative forms of causal relation between individuals that might drive selection in the same ways as competition (and perhaps with even more profound effects on outcomes). Competitive, cooperative and exploitative forms of selection were thus grouped together within my category of "strategic" selection. It might well be possible to define causally linked Darwinian populations relative to cooperation and exploitation in the same manner as competition.

However, such a possibility is moot, as I also set out a second category of "parametric" selection, which is driven simply by the interaction of individuals with their general, abiotic environment, rather than with one another. In such cases, we would not be able to define *any* Darwinian population via reference to competitive, cooperative or exploitative causal relationships between individuals, as none exist to be referred to.

I used Lewontin's bacteria as an example of parametric selection but noted that there was controversy as to whether that case ought to be counted as selective, due to its counter-intuitive nature (though I gave reasons in chapter one as to why we should regard such instances as valid examples of selection). As such, let us consider a causally analogous – but more intuitive – case here, which we can return to in subsequent sections.

Take the ongoing problem of the evolution of antibiotic resistance on bacteria[16]. If we conducted a lab experiment in this area, we might place two or more strains of some bacterium in a surplus of nutrients, just as in Lewontin's scenario. Now, though, we will subject the collection of bacteria to waves of various antibiotic agents. This will differentially kill off or reduce the growth rate of the strains, according to their ability to tolerate the various chemicals. If we ran this experiment for a sufficiently long period of time, we might also observe new, better-adapted variants arise by mutation and subsequently outperform their peers.

It would be difficult to deny that this kind of scenario is a clear instance of selection, despite sharing the same fundamental causal structure as Lewontin's Bacteria. In both cases, we simply see differential performance in prevailing conditions by variants that have no actual impact upon one another. In the case of antibiotic resistance, how one strain fares in the face of, say, an infusion of penicillin is not dependent upon anything its neighbour does or does not do, or whether that neighbour *is even present*. Clearly, then, criteria based upon competitive or similar strategic interactions will fail to define a Darwinian population *at all* in an important class of selective scenarios.

Even if we set aside these concerns about failure to extend to valid cases of parametric selection, defining the Darwinian population in terms of strategic interactions would also lead to what might be considered as overextension in other instances. Some instances of competitive selection will be inherently limited to conspecifics – sexual selection for example (at least under something like the Biological Species Concept from Mayr 1963). However, I see no principled way to exclude cases that share the same causal structure, but which cross species boundaries. For example, in competition, the

[16] An example suggested by Tim Lewens.

same kind of causal relations will hold between competitors for the same resource independent of any other facts about those individuals. Consider again our trees vying for light in a forest. The pressure for one tree to out-grow its neighbour will be just as fierce whether or not that neighbour is a conspecific or from a very distant clade. As per the same example in chapter four, a pine and a spruce might compete for light just as fiercely as two pines. Similar examples will be available for cases of cooperative and exploitative selection (such as Stegenga's 2016:9 example of cooperation between fungi and algae in the selection of lichens - also discussed here in section 3.1).

How one regards the prospect of multi-species Darwinian populations will depend upon one's wider theoretical commitments. As we saw in chapter four, Van Valen's competitive account of selection and fitness promises to allow for selection to occur and for fitness comparisons to be made between highly disparate, distantly related species, so long as they compete for the same resource. This is precisely by virtue of that author's identification of the Darwinian population with the set of competitors within what Van Valen (1973) calls a "resource space", and illustrates a following-through of that rationale.

Of course, Van Valen's scheme is not without significant problems and (as per Futuyma above) it is common to draw Darwinian populations exclusively from the same species (discussed in section 3.1). As such, the idea of multi-species selection might be intolerable for readers committed to that position and would give reason to regard Darwinian populations defined by reference to strategic interaction with suspicion. Certainly, though, one will not be able to straightforwardly maintain a conventional view of the Darwinian population by referring only to competition or some similar direct causal interaction. Whilst it might be imagined that such a criterion would function to pick out mundane groups of conspecifics, we see that this will not be the case. Thus, in its full implications, a definition of the Darwinian population based on one or some superposition of strategic interactions would be highly revisionary in itself.

Finally, it should be noted that strategic interactions like competition will not always be as direct as we might imagine. Often, selection will indeed be driven by interactions taking place between all members of a Darwinian population simultaneously. For example, as in chapter one (section two), when a herd of zebras flee from a lion, the whole herd is involved in a single race not to be the slowest. This will not always be the case, though. In my discussion of Van Valen's ideas of universal competition in chapter four (section 3.1), I noted that individuals within a population might each compete only with their neighbours. This would allow a chain of competitive relationships to span the population as a whole. However, I showed that the relationship of "being in competition against" is not sufficiently transitive to allow for individuals at either end of a chain of competitors to be meaningfully regarded as competing with one another. As such, A might compete with B and B with C, but this will not mean that A

meaningfully competes with C. This is not simply a semantic issue, but one with real causal implications when it comes to predicting the outcomes of competitive pairings. Thus (via analogy to the familiar "rock paper scissors" game), I explained that, if A outcompetes B and B outcompetes C, it will not necessarily be the case the A will outcompete C. The same can be expected to hold true for cooperative or exploitative relationships.

Thus, just because a population undergoes strategic selection, does not mean that all pairs of individuals will actually interact with one another. This is particularly relevant here, as it arguably undermines the desirability of defining a Darwinian population by reference to competitive, cooperative or exploitative interactions in the first place. Bounding a Darwinian population via reference to strategic interaction seems appealing on grounds that it ostensibly provides a direct and causally meaningful tie between individuals. However, the possibility that strategic interactions might only meaningfully hold between immediate neighbours reduces the causal linkage between many of the members of the resulting grouping to an indirect one. This might not be sufficient reason in itself to reject Darwinian populations based on strategic linkages, but it is certainly an additional point weighing against that approach.

1.2. Reproduction

One of the most commonly cited criteria for bounding a Darwinian population is the presence of reproductive interactions – as a direct causal linkage – between its members. For instance, Godfrey-Smith (2009, chapter one) notes the apparently sensible idea that, if natural selection is fundamentally concerned with the business of reproduction, then reproductive relations seem a good starting point for delineating the group of organisms involved in an instance of selection[17]. This way of defining the Darwinian population elides heavily with ideas that entities under selection together ought to be drawn from the same species (examined in section 3.1). Certainly, the significant traction of the Biological Species Concept (Mayr 1963), means that reproductive linkage and species membership are often considered as near-equivalent ideas.

In chapter two, I argued against the exclusive relevance of reproduction to selection, pointing out the importance of growth and longevity as components of fitness. As such, I obviously reject the basis of this sentiment from Godfrey-Smith. However, I also realise that this view is far from the consensus. Fortunately, it is possible to reject the idea that reproductive linkage should be definitive of the Darwinian population without reference to anything as controversial as selection for longevity or somatic size.

[17] As noted above, my own suggestion that selection might also function in terms of longevity and somatic growth conflict with this idea, and might encounter problems with an exclusively reproduction-based Darwinian population concept.

It is true that there are a great many cases of selection that are driven, or greatly influenced by, causal interactions stemming from the reproductive relationships between entities. However, these cases will all concern sexually reproducing species. It is an oft-repeated point that the Biological Species Concept, which defines a species via the ability of its members to produce fertile offspring together, is dysfunctional for asexual species. In such species, there need be no causal interactions *at all* between conspecifics for reproduction to occur. Given that the majority of life forms reproduce asexually, we would presumably like our account of natural selection to extend to them. As such, we cannot possibly insist on reproductive linkage as a necessary criterion for membership of a Darwinian population. Even if we included reproductive connection as a "plus point" to delineate a "paradigm" Darwinian population in an account like Godfrey-Smith's (2004), we would have to reconcile ourselves to the fact that it will not be relevant to *at least* the bulk of species made up by asexual forms.

Even within sexually reproducing species, though, we should note that reproductive linkages might not do much to causally bind specific entities we would wish to consider as under selection together. Thus, just as with strategic interactions, even where a chain of reproductive links between individuals might transect a population, it does not mean that every individual will be meaningfully causally bound to every other.

As for a herd of zebras escaping a lion, there are some cases of competition and similar strategic interactions which will concern a whole population simultaneously. With reproduction, though, an individual will only ever directly interact with a small subset of its peers. Indeed, this may or may not coincide with the group we would like to say that individual is being selected alongside. For something of a limiting case, consider ring species (for example, the greenish warbler of Ticehurst 1938). In such species, not all conspecifics are reproductively compatible. Where the two "ends" of the ring species abut one another, we observe members of the same species which cannot reproduce together, but which might well undergo other causal interactions with one another, such that we wish to regard them as under selection together. Thus, we might observe selection as a result of competition for food or other resources between conspecifics that cannot reproduce together. In principle, these individuals do have some reproductive linkage between them, but it is a particularly indirect and likely causally insignificant one. If W and Z are at the two ends of a ring species, they are linked reproductively only in that W breeds with X, X breeds with Y and Y breeds with Z. W will not be able to breed with Z. In effect, we are relying upon some transitive property of "being reproductively linked" to place W and Z in the same Darwinian population. This does not seem sufficient to ensure much of a relationship between specific individuals at all - let alone a direct one.

1.3. Reproductive Competition

I have already noted, both in chapter one and in section 1.1 here, that zero-sum competition is not a universal feature of natural selection and will thus fail to define Darwinian populations for many cases of selection. Additionally, we have just discussed the failings of reproductive relationships between individuals to bind those under selection. As such, reproductive competition already seems like an unsuitable criterion by which to define Darwinian populations.

However, the idea that selection involves some inherent competition for representation in the next generation is so persistent that I should explicitly deal with it separately. Indeed, there seems to be a perception that this kind of competition occurs regardless of any resource competition or sexual selection, as some kind of separate category of competition.

I take these ideas to be simply misguided and explain in chapter one that I see them as resulting from a human tendency to describe any difference in performance as the product of competition, regardless of causal reality. Thus, when we notice that one type has produced more offspring than another, there is a habit of describing the more fecund variant as having outperformed its peer in some competition, regardless of whether they causally interacted at all. I have previously discussed (in chapter one, section one) how the difficulties in mapping a human term like competition onto the natural world leave room for disagreement over how to proceed. Simultaneously, though, I pointed out that competition defined in such a weak fashion would apply so widely as to become a meaningless description.

Ultimately, cases of parametric selection amongst asexual organisms – such as our antibiotic resistant bacteria – should be sufficient to rule out any necessity for reproductive competition in grouping individuals under selection. These cases clearly demonstrate that selection can act without the presence of meaningful competitive or reproductive links between members of a Darwinian population.

2. Indirect Causal Connections

As we have seen, aspirations to define the Darwinian population in terms of any direct causal linkage between individuals are consistently foiled by the existence of clear instances of selection where no such relations hold between participants *at all*. Even taking the superposition of any and all direct causal relations would not be sufficient to define a Darwinian population for asexual cases of parametric selection (such as our antibiotic resistant bacteria). As such, I will move on to examine ideas that members of the Darwinian population share somewhat weaker, "indirect" causal interactions. Under

this kind of approach to defining the Darwinian population, those entities under selection would not necessarily interact with one another, but would share causal influences in common.

2.1. Shared Environment

Ostensibly, the most obvious way for members of a Darwinian population to possess an indirect causal connection to one another is to inhabit the same environment. Different readers might take a stipulation of shared environment to mean slightly different things. Many will regard it as a requirement that individuals experience the same environmental conditions as one another. Others will take the idea of a shared environment to mean that individuals inhabit the same geographic locale. I will deal with both ideas here.

2.1.1. Shared Conditions

That those involved in the same instance of selection are subject to the same environmental conditions is assumed so frequently that it could almost be taken as a requirement prior to defining a Darwinian population. In many cases, though, shared conditions do seem to be a sensible way to pick out that grouping. Our antibiotic resistant bacteria, for example, might be considered under selection together by virtue of their both being exposed to the same toxic compounds and the same general conditions (temperature, pH, salinity and the like).

Our intuitions here are strong and seem to be linked to ideas of competitive fairness and fair comparison. Thus, it would indeed seem "unfair" or "misleading" to claim that we had seen selection for some entity, which had been successful by virtue of experiencing particularly benign environmental conditions, over some otherwise similar peer that had been unsuccessful as a result of highly unfavourable conditions. To take a simplified example, say we observe two hedgehogs that both start from the same location and walk in different random directions (determined simply by chance, without any preference by the animals). One hedgehog finds itself in a hospitable wooded area with plenty of food and shelter, whilst the other ends up in the middle of a motorway during rush hour. The two hedgehogs will likely enjoy very different levels of subsequent reproductive success (likely zero for the latter animal). However, very sensibly, we would not be comfortable describing these differences as the result of selection. It would feel like we were simply not comparing "like-with-like" in the appropriate manner.

I will elaborate on our intuitions around uniform environments and ideas of fair comparison in section five. Here, though, it should be sufficient to point out that the requirement for members of a Darwinian population to share the same environmental conditions is something of a red herring. As Brandon (2014:§3) points out, in the real world, we should not expect that *any* two

individuals will ever experience *precisely* the same environmental conditions[18]. Real-world environments are not bubbles of perfectly even and stable conditions. Rather, conditions will vary stochastically over both space and time. Even if they inhabit the same environment as defined by a probability distribution of different states, individuals will all experience different states of that environment in different sequences. As I will return to in section five, differences in environmental conditions experienced by individuals might confound our ability as observers to determine the contribution of selection to the success or otherwise of individuals, but we must not conflate this with the idea that those differences in environment will somehow prevent selection from occurring. If we were to require truly uniform environments for selection to occur, then we could no longer perceive *any* cases of real-world selection, as no two individuals will ever experience *precisely* the same conditions.

2.1.2. Spatial Proximity

Certainly, putative cases of selection where members of the apparent Darwinian population do not inhabit the same geographic location can seem highly counterintuitive. Lewens (2010:831) gives the example of two herds of the same species of reindeer, one living in Sweden and the other in Canada, where one herd has a higher rate of reproduction than the other. Even though they are conspecifics and one herd is better adapted to identical environmental conditions prevailing across both locations, many have an intuitive objection to the reindeer being regarded as under selection with one another, due to the great distance between them, with an idea that things might be different were they in the same place.

However, as intuitive as the spatial proximity idea is, it is easily dismissed as definitive of the Darwinian population. Stegenga (2016:9-10) points out the vague nature of any proximity requirement. Even if we allow that the distances concerned will vary between different kinds of lifeform, there is still no way to establish exactly *how* far removed is *too* far for two entities to be considered members of the same Darwinian population. What is left is a very arbitrarily bounded grouping.

Generally, though, if we consider why we are so attached to the idea of spatial proximity, it is invariably because we want entities to interact with one another in some way. Lewens thinks that it is the consequent lack of interaction, rather than spatial separation *in itself*, that makes

[18] Brandon himself does not regard this as problematic, allowing for environments to be sufficiently similar as to be equivalent where they generate the same "ordinal relations in fitness of the competing types" (2014:§3). However, I have already argued across previous chapters both that selection need not involve competition and that objective ranking of types under selection is not always possible. Thus, I regard those previous discussions as sufficient to counter Brandon here.

his reindeer example so seemingly implausible as a selective scenario. Whilst it might be necessary for direct interactions, though, spatial proximity is far from sufficient to ensure that these occur. Once again, returning to instances of parametric selection amongst asexual organisms, we can readily find examples of selection where entities might inhabit the same area, but where they do not interact in any selectively relevant fashion. As mentioned, Godfrey-Smith (2009:§3.3) notes that there is no difference in the behaviour of the strains of Lewontin's bacteria as they are moved further and further from one another. In short, then, spatial proximity has no inherent bearing on selection and is desired only as a proxy for causal interaction – which we have seen to be problematic in itself.

2.2. Shared Ancestry

Common ancestry can be taken as a second form of indirect causal relationship potentially holding between members of a Darwinian population. Individuals might not interact with one another at the present time, but would be united by descent from a common ancestor. In many cases, common ancestry might track or act as a proxy for other factors we considered here, such as reproductive linkages or membership of a single species (examined below). Taken strictly in itself, though, shared ancestry is fairly meaningless as regards selection.

A key idea from Darwin's *Origin* (1859) was that life on Earth emerged from a single or a very few common ancestors. Today, it is common to believe that all lifeforms so far observed are end-branches on a single, common tree of life. With this in mind, though, it becomes difficult to see how shared ancestry could be a particularly relevant criterion in itself when deciding whether a certain subset of organisms are under selection together. As long as it remains our standing assumption that all life on Earth shares a common origin, selection between *any* group of organisms will necessarily be between individuals with a common ancestor.

Certainly, there will be very large differences in how *closely* related individuals will be. However, this will unavoidably be a matter of degree and, as such, it becomes difficult to define where a cut-off value should be, such that individuals are too distantly related to be in the same Darwinian population. Thus, as in the case of spatial proximity above, we face the standard problem of trying to impose a binary distinction on phenomena existing on a spectrum. In the case of shared ancestry, the likely fallback would be to ideas that the correct degree of relatedness would ensure one of the other causal relations – such as reproductive linkage – which I show to be problematic in other sections.

Of course, problems in making a criterion workable do not necessarily indicate that the criterion itself is incorrect (indeed, one could take a position like Godfrey-Smith's or Stegenga's allowing population

membership by matters of degree). However, Stegenga (2016) provides a more direct argument against common ancestry being necessary for selection to proceed *at all*. Thus, Stegenga uses the thought experiment of a "swamp species" – a set of newly constructed biological automata, able to reproduce with one another and so on, just like conventional organisms. Despite not being part of a lineage at all, these automata will undergo selection and evolution as a group, demonstrating the irrelevance of ancestry for selection. Similar arguments are deployed in support of relational essentialist definitions of species, where it is noted that a newly created organism manifesting the correct traits could seamlessly integrate into a species, despite sharing no ancestry with its peers (Godman 2018, Ereshefsky 2017).

To this, I would add the real-world example of genetic diseases like Huntington's. The single mutation causing Huntington's can either be inherited from a parent or independently occur *de novo* in an individual but will confer the same detrimental, fitness-reducing effects regardless. Thus, the relevant genes are selected together in the wider gene pool, regardless of lineage (llarioshkin et al 2018, Houge et al 2013).

To reverse matters, the phenomenon of speciation demonstrates that even millions of years of shared ancestry will not prevent a group being split by selective pressures and sent down two very different paths at any time. As such, we see that shared ancestry is neither necessary nor sufficient for entities to undergo selection together.

3. Other Factors

We can see that there are major problems in defining the Darwinian population via *any* causal criteria. Indeed, it is readily possible to come up with cases that cannot be accounted for even by a superposition of *all* the criteria which I have examined thus far. Notably, for cases of parametric selection of asexual organisms in a typical stochastic environment, it appears to be impossible to consistently define Darwinian populations in any causally meaningful manner.

As such, I will examine the possibility of bounding Darwinian populations via a few other relationships that often have a good deal of stock placed in them, despite not necessarily implying causal linkages between individuals. In practice, these will often be associated with, or be taken as a proxy for, one or more of the causal links which I have already discussed but, for the sake of thoroughness, I will analyse them as criteria in their own right.

3.1. Species Membership

Species is an ill-defined term. Real-world species can also be ill-defined, with largely arbitrary differentiations made for many asexual cases, as well as often highly indistinct boundaries in sexual cases where hybridisation is possible or speciation is only half complete (Ereshefsky 2017 provides a general discussion). The causal relevance of species membership also varies a great deal in different taxa. As such, species is generally – on both principled and pragmatic grounds – not an ideal concept on which to base an important, fundamental notion like that of the Darwinian population.

Given Millstein and Stegenga's remarks as to the Darwinian population being a more fundamental concept for selection than that of species, we should also be suspicious of attempts to define the Darwinian population in terms of species membership. Indeed, such suspicions rapidly prove justified when we perceive the problems in doing so.

Depending how one defines species membership, conspecifics might be thought of as bound to one another by various causal relationships. Thus, we might expect the requirement of species membership would imply, or act as a proxy for, reproductive linkage via something like Mayr's Biological Species Concept. Similarly, we might imagine conspecifics to be in reproductive competition with one another (as per Ghiselin 1974), or perhaps to undergo resource competition within a particular adaptive niche. As it is, though, I have already dealt with all of these kinds of causal interaction directly in the sections preceding this one – with all having proved problematic. Even setting aside each criterion's own unique issues, I have demonstrated that any such causal criteria will inevitably fail to delineate Darwinian populations for simple parametric cases of selection – like our example of differential antibiotic resistance in bacteria.

It is not clear what membership of a single species could offer beyond such causal links. However, as with reproductive competition in section 1.3, membership of a single species is so commonly assumed as necessary for membership of the same Darwinian population that I feel the need to address the idea separately. In fact, we can quickly rule out the idea of imposing this requirement upon Darwinian populations, due to the possibility of real instances of selection occurring across species boundaries. I have already discussed the idea that cases of strategic selection frequently seem to involve members of multiple species – with particularly clear examples in the case of competitive selection (for example, the competition for light between different kinds of tree, mentioned in section 1.1). In chapter four, Van Valen's account provided an example where Darwinian populations are defined as such. In a similar vein, Stegenga (2016:8-9) gives the example of lichens as a cooperative relationship whereby two species appear to undergo selection together. Whilst lichens resemble plants, they are actually a

mutualistic partnership between fungi and algae, where one species can be dependent upon the other even to reproduce.

These examples may have too much of a revisionist flavour for many readers, in that they require moving away from a typical understanding of selection and fitness to appreciate them. As such, it is useful to demonstrate potential selection across species boundaries whilst keeping to a conventional account of selection as far as possible. This can be done by applying a standard gene-selectionist framework (as per Dawkins 1976 and Hull 1980).

Stegenga (2016) points out that the same allele can be found across different species. As such, he suggests that, if selection is taking place between alleles, then the relevant Darwinian population will range across the various species in which those alleles are present. Stegenga uses an example of gene-level selection from Sterelny (2009), where alleles will distort sex ratio in their favour if they are more likely to be found in offspring of one sex rather than the other. To elaborate slightly, genes might continue to be present and to be selected for the sex biases they produce in meiosis, whilst selective pressures at the level of the whole organism cause speciation – both resulting species retaining copies of the same genes. From our focal genes' "point of view", nothing much has changed as a result of this new partitioning of the population, and they will continue to be selected for or against for their action at the cellular level.

Other means for genes to cross between species would include the oft-cited phenomenon of horizontal gene transfer between micro-organisms. At the more familiar macro scale, hybridisation in sexually reproducing organisms will often result in gene flow between species, though will admittedly tend to be limited to members of the same broader clade. The action of retroviruses, such as HIV, provide a neat example of genes being newly spread between potentially distantly related species (and certainly in cases where hybridisation is not possible) at the familiar "macro-organism" scale. Retroviruses permanently[19] implant a stretch of DNA in their host organism's genome, forcing cells to produce more virus particles. It is possible for the same retrovirus to infect multiple species, as observed in the infamous spread of the HIV virus from apes to humans, and thus for the same genes to be implanted into the genomes of only distantly related organisms. As above, in the case of meiotic drive, the gene's "cell-level" point of view will remain more or less unchanged across the different species where it acts.

[19] The permanence of this implantation is important to our example here. Some might discount this case as constituting cross-species selection, as selection appears to be limited to one viral lineage – and so effectively to one species. However, once the new gene is implanted in the genome it remains permanently integrated, even undergoing mitosis. As such – at least for thinking about our point of principle here – we can hopefully treat the genes as effectively "belonging" to hosts of different species, as if it had emerged there by mutation. Certainly, we know that substantial parts of our genomes are made up of former viral DNA and that these genes can be recruited to new functions, so questions of the "ownership" of genetic material become blurred over time.

Retrovirus genes will be selected according to their ability to force host cells to produce more copies of themselves, just as sex-ratio distorting genes will be selected for their ability to influence meiosis, regardless of which species' genome they are found in.

This application of the usual gene-selectionist framework might still be too exotic for some. For one thing, it is common for gene-selectionist accounts to confine selection to a single species, often via the idea that alleles ought to be thought of as competing for future representation within a particular discrete gene pool. These examples, whilst compatible with the framework in general, would be ruled out by such an initial stipulation – though, I have already argued against the meaningfulness of the idea of competition for representation in future gene pools or populations (in chapter one and also in section 1.3 here), which undercuts at least one major justification for a single-species account of gene-level selection.

Nevertheless, it is pointless to begin a long discussion as to specific interpretations of gene-selectionism. I have shown that positive work will be required to put forward a single-species criterion for Darwinian population membership. This work would also be far from straightforward. There would be a need to demonstrate that selection is properly confined within single species. To do so would require ruling out apparently sensible cases of gene selection across species – such as Stegenga's of alleles for meiotic drive and my own of selection for retrovirus alleles. On top of this, it would need to be shown that the whole host of cross-species strategic interactions are similarly invalid. This would mean – for instance – explaining why two conspecific trees vying with one another for light are under selection, whilst two trees of different species engaged in the same behaviour are not. Even with all this achieved, it would still fall to those proposing a single-species Darwinian population to demonstrate that species membership is meaningful *in itself* rather than simply acting as a proxy for some causal relationship that might be specified directly.

3.2. Similarity

One major motivating factor for requiring that members of a Darwinian population derive from the same species is an idea that individuals under selection together should be similar to one another. Indeed, various definitions of species attempt to define that category as some function of phenotypic similarity. Whilst unfashionable amongst theoreticians, broadly phenetic approaches do have some utility in the real-world business of defining species in certain taxa – notably in the bacterial realm (Lewens 2012). Ensuring that those in Darwinian populations are similar to one another helps avoid apparently absurd cases where we attempt to make sense of selection between totally disparate organisms. Imagine, for example, trying to compare the reproductive output of the average human to that of a common rat. The rat will obviously reproduce vastly more quickly, with only the briefest of

intergenerational times, whilst all the offspring a human produces in their whole lifetime will likely be less than the number of pups in one rat litter. Surely, one might say, the two species are too different to be meaningfully compared in terms of number of offspring. How can we really learn anything from the comparison of the many thousands of tiny pups one rat lineage might produce over a couple of years to the handful of children a human lineage produces over several decades? Certainly, it is not at all clear that the higher number of descendants means the rat is "outperforming" the human or "winning" in any competition. Thus, intuitively, it seems that we should want to ensure comparability by keeping selection within one species.

However, as noted in chapter two, it is a mistake to think that conspecifics need to be particularly similar to one another. For instance, at the phenotypic level at least, polymorphisms can make for enormous differences in all manner of traits between members of the same species. A particularly vivid example is found in the vast differences in both size and form between the male and female angler fish, where the female is a great many times larger than the male (Regan 1925, Vollrath 1998). In many cases, an individual might be closer in terms of basic physical quantities like mass or energy usage to equivalent forms in a closely related species. Thus, workers from two ant species might be more physically comparable to one another than to either their own queen or soldier conspecifics.

Beyond raw, physical polymorphisms affecting body configuration or size, it is also possible for traits like lifecycle or intergenerational time and offspring number to vary widely between different populations of the same species as an adaptive response to different environmental conditions. In this fashion, some species will produce smaller numbers of more robust offspring as they transition from the harsh general environment of an r-selected context to the competitive demands of a K-selected regime (for example, see Reznick, Bryant and Bashley 2002 on the variable life history of the Trinidadian guppy). All of these sources of intra-species variation across any quantity one might regard as salient means that requiring members of the Darwinian population be drawn from the same species is a poor way to ensure those members' similarity.

Even without polymorphism, there can be very significant differences between conspecifics. We can find huge disparities in various "unusual" species, and I have previously drawn attention to the enormous differences in biomass and/or longevity that might obtain between individuals within species of the *Armillaria* genus of giant fungi, the “immortal” jellyfish *Turritopsis dohrnii* and between groves of quaking aspen (all discussed in chapter two). However, even in more "familiar" species, variation between individuals can be very large. For instance, within a small human population, one would not need to look far to find two adult males where one was twice the bodyweight of the other.

It would obviously be difficult to hold that these dissimilar conspecifics should never be placed within the same Darwinian populations. Confronted with such cases, it might be tempting to ignore certain differences between individuals and instead state that members of the Darwinian population are such by virtue of some set of important underlying similarities. However, nature abounds with clear and important cases of selection between highly dissimilar types, where that selection obtains precisely *because* of the large differences between those types.

Selection maintaining balance between the frequencies of different polymorphisms provides some of the clearest examples of selection between disparate conspecifics as a *result* of their disparities. In this vein, we could take the example of stabilising selection maintaining a constant sex ratio (as per Fisher 1930, explained in chapter three section 2.2.1) as an instance where potentially highly physically distinct sexes are clearly in the same Darwinian population. Even more vivid illustrations are found in cases like that of the competitive sexual selection between the polymorphic males of the common side-blotched lizard. Here, males are physiologically and behaviourally highly different, pursuing distinct mating strategies. Thus, the smallest males mimic females and attempt to "sneak" matings amongst the harems of the largest (Sinervo and Lively 1996, Zamudio and Sinervo, 2000). Understanding these variants as under selection against one another allows us to understand fluctuating population dynamics that emerge between them. In principle, there is no upper limit to the degree of difference between entities that might be profitably considered in a similar fashion. As such, we not only see that being from the same species is a poor guarantor of physical similarity but also that similarity is often irrelevant to selection, despite some of our intuitions to the contrary.

We can think about these issues at a slightly more abstract level. So far, we have considered cases where similarity is minimised, such that individuals are highly distinct from one another. However, we can invert this and consider a Darwinian population where similarity is maximal, such that individuals are identical, indistinguishable copies of one another. Were this the case, natural selection in any conventional sense simply cannot occur. Whatever theory we subscribe to, at its core, selection will necessarily be some function of the differential performance of individuals or types. If all individuals are identical, there can be no systematic differences in biological success between variants and thus no selection.

Of course, in this hypothetical population, individuals might still have different fates as they interact with a stochastic environment or are otherwise differently affected by probabilistic events. We might think of these differences in success as differences in realised fitness, where individuals all have identical expected fitness. However, the resulting changes in the population will not be explicable by selection and could only be taken as examples of drift. This necessity should hardly be surprising. There

is good reason for the presence of variation as a foundational requirement for natural selection across various different schematic accounts (most notably in Lewontin's 1970 Heritable Variation of Fitness criteria). Thus, we can see that some irregularity/heterogeneity is required for selection to operate *at all*. As such, it seems unwise to make similarity a prerequisite for membership of Darwinian populations.

By the same token, though, our instinct to avoid Darwinian populations composed of vastly different kinds of individual remains a strong one. My example above, comparing the reproductive success of a human with that of a common rat is so obviously invalid a case of selection as to be whimsical. I do not think that we should simply ignore this apparent tension between a desire for homogeneity and a need for heterogeneity. Rather, I think that appreciating this tension is crucial for our understanding as to why the Darwinian population has been so difficult to define and will be explored in section five.

4. Findings

By this point, we have exhausted our options as to finding a singular way of defining Darwinian populations in anything like the conventional mould. Having examined direct and indirect causal links, as well as other commonly cited ways of bounding Darwinian populations, we have found no universal criterion by which to meaningfully bind the participants in instances of selection; and indeed have not found any way *at all* to meaningfully and reliably link asexual individuals involved in cases of parametric selection.

Our immediate, instrumental response to this state of affairs must be some manner of pragmatic pluralism, whereby we choose different ways to define Darwinian populations in different scenarios. As with my own pluralist approach to fitness in chapter two, a pluralist approach to the Darwinian population will require the development of a conceptual scheme to appropriately constrain these choices and render the resulting groupings non-arbitrary and meaningful. Stegenga (2016) has already embarked on this task and I will not consider the specifics of this issue further here.

One positive outcome of there being no universal, monist account of Darwinian populations is that my discussion across previous chapters can stand as-is. There is no threat of a blanket requirement for members of Darwinian populations to have competitive, reproductive or other such causal linkages which might rule out my points on competition and fitness as explained above.

Rather than delve into fleshing out a pluralist approach to defining Darwinian populations when this has already ably handled by Stegenga, I will now take another direction and pick up on some of the conflicting intuitions we have noted around Darwinian populations to consider one reason why that concept has been so resistant to simple analysis. In short, I will hold that some measure of this difficulty is because we frequently conflate Darwinian populations with another kind of grouping we make when assessing instances of selection.

This idea will not aim to supplant the pluralism I have just referred to, but is intended to supplement ideas around Darwinian populations and could readily be merged with Stegenga's work. My points simply put forward an additional kind of grouping to consider when we think about selection, and one to avoid conflating with Darwinian populations.

5. Comparison and the Darwinian Population

The second kind of grouping I propose does not gain its meaning via causal salience to the outcomes of that instance of selection, as per the conventional idea of Darwinian populations. Rather, these groupings are made to facilitate comparative inference as to the action of selection, with these inferences then supporting explanation and/or prediction. Crucially, as we will see, this requires no causal or other necessary linkage between members of the resulting group. However, mistaking some of these inferential groupings for Darwinian populations often leads us to seek out causal connections or similar between individuals where these bonds might simply not exist, and generally confounds our Darwinian population concept by making it account for instances of something else.

To explain more fully, let us start from the conflicting intuitions we noted previously. In the course of discussion, we ran into strong feelings that Darwinian populations ought to be situated within a homogeneous environment and that their members ought to be similar to one another. Generally, then, we find the recurring idea that Darwinian populations should be broadly "uniform". This uniformity seems to prevent us from making variously absurd, unfair or invalid comparisons between individuals. We might say that uniformity ensures that we compare "like-with-like". Simultaneously, though, I have noted both that selection can still occur without a uniform environment and indeed that selection seems impossible in the absence of a degree of variation within the members of the Darwinian population. Thus, selection can both occur *in spite of* irregularity and indeed seems to *require* a certain degree of such non-uniformity.

The intuitive desire to restrict how we bound Darwinian populations in line with concerns about fairness or valid comparison is an interesting one. Generally, whether or not a process is fair is a secondary consideration to the question as to whether that process is occurring in the first instance. Thus, I can know that I am participating in a game without being sure whether my opponent is cheating or not. If it turns out that they have indeed been cheating – so that the game was not fair – it does not change the fact that the game was played. Similarly, selection will be ongoing regardless of whether conditions are sufficiently uniform for us to able to fully appreciate what is happening and to make "fair" comparisons between participants. Thus, the traits manifested by individuals will accord them a certain degree of success in the conditions they experience, whether or not other individuals experience particularly similar conditions and whether or not those individuals are particularly similar.

So, why do we seem to care about uniformity? I believe we can find the answer in considering what we actually use Darwinian populations for. Introducing this chapter, I noted that Millstein (2009) was concerned that we should arrive at a proper definition of the Darwinian population so as to ensure that we are making correct inferences as to the action of selection. Whereas Millstein then goes on to attempt a definition of the Darwinian population from consideration of the nature of selection itself, I think we might do better by remaining with this idea of inference and working outward from there.

To illustrate, let us consider how we might infer the contribution to fitness of a particular trait based on the realised fitnesses of those bearing said trait (allowing us to then explain or predict how bearers of that trait have fared or will fare in selection). To start, say we are were dealing with the imaginary, perfectly simple case where individuals are absolutely identical except in terms of whether or not they possess our focal trait. The individuals also inhabit a completely uniform, unchanging environment. Finally, we can also specify that our individuals reproduce asexually, to remove complications there.

In this case, it will be very straightforward to establish the contribution made by individual traits. Perhaps, like Kettlewell's (1955) moths, one variant is light and one dark, with the dark being the fitter. The absence of any irregularity here removes any possibility of drift and renders the realised fitness of all individuals of a certain type identical. All dark individuals will exhibit the same biological success as one another and all the light individuals will exhibit equal realised fitness within that group. Thus, to understand the difference made by the possession of dark rather than light patination, we will simply have to inspect the realised fitnesses of one dark and one light individual. We can then ascribe any difference in biological success between the types to the difference in patination.

Of course, the natural world is never this simple. At a minimum, individuals will always experience at least slightly different sets of environmental conditions. Say, then, that we place our idealised

population in an environment subject to the sort of stochastic variation described by Brandon (1990, 2008). Now, the realised fitness of individuals of the same type will be subject to variation and we cannot make reliable inferences about the contributions to fitness of a trait via such a simple comparison. Even if dark patination is generally fitter than light, we might very well select a pair of individuals where a light individual leaves many offspring whilst its dark peer dies before reproducing at all.

For us to understand the casual contribution made by patination, we will now have to account for environmental variation by taking an average of biological success across multiple dark individuals and comparing this to an equivalent average across multiple light individuals. The larger the number of individuals of each type we consider, the more accurate we can expect our answer to be. In the extreme case, where we examine an infinite population of both types (such that drift disappears) we can once again be sure of the exact mean contribution made by each trait in which we are interested.

Accounting for the effects of environmental variation is not the only reason to make inferences via comparison across groupings of multiple individuals. Thus, we can return to the idealised, perfectly constant and uniform environment we began with above. However, now we can allow for our individuals to vary across multiple traits simultaneously. Perhaps we can imagine that our organisms now vary not only in terms of patination but also in terms of body size and limb length. Of course, in any real population, individuals will likely vary in terms of vast numbers of different traits simultaneously, so this remains a huge simplification versus biological reality.

In this new case, if we want to understand the contribution made by having, say, long-limbs as opposed to short, even in a uniform environment, we cannot simply compare the realised fitness of a single, long-limbed individual against that of a single short-limbed peer, unless the pair happen to be identical across all other traits. Where such near-identical individuals are not available, though, we must make comparison across a number of different individuals to be able to isolate the contribution of a single trait (thus, we might round up a large, pale short-limbed organism along with a small, short-limbed dark one and so on to make our comparisons).

In a more realistic population, finding two individuals which differ in only one trait will almost certainly be impossible – the rarity of the chance to at least minimise variation between individuals is precisely why twin studies are so incredibly valuable when studying human populations (Boomsma, Busjahn and Peltonen 2002). Indeed, in a real population, the sheer number of points of potential variation makes it important to establish large groupings (and, of course, any real population will always be subject to environmental variation, which will also require large groupings to account for, as noted).

Across all these examples, then, we assemble a grouping of individuals by which to make comparative inferences with much the same rationale as we might lay out a set of simultaneous equations in order to find the value of some variable in a system with multiple unknowns. In both cases, as we increase the number of variables, so we must increase the number of elements in our comparative set – whether this be equations or individual organisms – required to take account of those variables.

As a shorthand, I label these groupings "comparative populations". As readers might have already noted, these comparative populations we are assembling to make our inferences look very much like Darwinian populations. Importantly, though, they are logically separable. We are selecting the comparative populations we do for this more pragmatic purpose of inference, rather than with the idea that members are necessarily linked to one another in a causally significant manner. Instead of being bound together so that they influence one another's selective outcomes or similar, the group of entities we are identifying here is simply one which we find it enlightening to compare to one another, so as to better understand the causality at work in the scenarios in which we are interested.

In many cases, a familiar, "traditional", causally bound Darwinian population will also happen to make a perfect comparative population. Say some physically larger variant prospers via outcompeting its conspecifics in zero-sum competition; outmuscling them in some tussle over resources, for example. We can clearly infer the contribution made by the trait of being larger and do so by reference to a grouping that also happens to be a causally bound Darwinian population. To spell this out, we see how the physically larger variant's performance compares to its smaller peers (a relevant comparative population) and can also note that they are all causally bound together by virtue of being in direct competition, by inhabiting the same locale and via reproductive links if they are sexual reproducers (common criteria defining Darwinian populations).

Where comparative and Darwinian populations elide in this fashion, no problems emerge. However, in some cases, comparative and Darwinian populations start to diverge and lead to confusion in the process. Possible examples here include when we group together the two strains of Lewontin's Bacteria, or the variants in our example of selection for antibiotic resistance. I would contest that we are making these groupings primarily in a comparative mode and not because the strains share some mysterious fundamental connection to one another. In short, when bacterium A resists penicillin better than B and only differs from B in possessing additional trait p, we can infer that A is being selected in virtue of its having trait p and that B's fitness is reduced for its lack of p. We do not need to believe that A and B are causally connected to make this inference – but we have mistakenly believed that they are, with much resulting confusion.

This idea of a comparative population allows us to make sense of a good deal of the difficulty we came across earlier as we surveyed possible connections between members of Darwinian populations. In cases like that of our antibiotic resistant bacteria, we encounter groups of individuals that we would certainly like to regard as undergoing selection together, but where we seem unable to find suitably meaningful relations between those individuals in order to do so. I would suggest that our interpretation of such scenarios is confused, as we are effectively assembling a comparative population, but attempting to interpret it causally. This confusion has been damaging, having spurred authors to undertake conceptual gymnastics in order to claim that these scenarios are not actually selective at all. Thus, we have already encountered the example of Lennox and Wilson (1994, discussed in chapter one) developing a dysfunctional account of struggle in order to rule out apparently perverse cases like Lewontin's Bacteria.

That comparative and Darwinian populations are indeed separable becomes clearest where they diverge more noticeably. Pure comparative inference allows for groupings of organisms which we would never wish to consider as being causally involved with selection together, but whose comparison is nonetheless enlightening.

For some, Lewontin's bacteria will already be an example here, in that many already refuse to hold that the two strains are under selection together, even if we might usefully compare them. However, Lewens' (2010:831) reindeer might also be grouped together into a comparative population, even if we would never wish to regard them as being sufficiently causally linked to be part of the same Darwinian population. Thus, we might very well wish to compare the biological success of two variants of the same species of reindeer exposed to the same environmental conditions, even if they are spatially very far removed from one another. The distance involved is irrelevant in itself to the profitable comparative inferences that we can make.

These kinds of more "distant" comparisons are particularly useful where traits have already gone to fixation within the immediate population and we wish to understand why selection stabilises that particular trait rather than an alternative (similar remarks found in Huneman 2012). In such cases, it can be useful to make comparisons even between members of more or less distantly related species. One area where this kind of comparative work is particularly common is behavioural ecology. There, it is typical to take a broadly "adaptationist" approach; assuming observed behavioural phenotypes to be optimal, with the investigator's task then being to explain how exactly this optimises bearers' success. Inter-species comparison can be highly useful in this context. An example is the use of the abstract "central place foraging" model to explain the specific observed food-gathering behaviours of multiple bird species as optimised for those species' particular circumstances (Orians and Pearson 1979,

Schoener 1979, Bryant and Turner 1982). There, we gain an understanding of each species' foraging behaviour by comparison to others.

Outside behavioural ecology, Huneman (2012) also provides a useful example of cross-species comparative explanation for the asymmetric feeding anatomy of the snake *Pareas iwasakii* – confirming that this is a specialisation for efficient predation of snails. This is inferred via comparison between closely related species relying on alternative prey, as well as more distantly related species which predate snails and are similarly adapted (Hoso, Asami and Hori 2007).

Overall, then, recognising comparative populations as a separate grouping lets us make highly enlightening comparisons, such as between Lewens' herds of reindeer, without necessarily having to worry about finding some kind of mysterious connection binding the animals together across thousands of miles or otherwise about how our Darwinian population concept might accommodate such a grouping. We can also explain at least some measure of our previous intuitions about similarity as a desire to seek out maximally useful comparisons, where individuals differ in as few traits as possible besides the focal one, so as to facilitate inference.

6. Directions for Development

The above points are sufficient as a brief sketch of how we tend to use comparative populations, how these can be conflated with conventional Darwinian populations and the kind of confusion that can result. Further work would be required to fully elaborate the idea of comparative populations, the finer details of their use and how they relate to conventional Darwinian populations. However, we can also add a couple of further directions for development.

6.1. Beyond Comparison

When I discuss how we might make inferences by comparing across groupings of individuals, readers might note that comparison is not the only means to make such inferences. In particular, some of the same inferences could be made via "engineering analyses", where we make use of our understanding of relevant physical laws and processes to understand causation directly, rather than via comparison to other entities.

Indeed, the comparative mode of inference will only take us so far on its own. Bouchard and Rosenberg (2004) note that some direct assessment of causality will ultimately be essential to differentiate the action of selection and drift. Their points are embedded in a wider argument about ecological fitness

and so are pitched in terms of the solution of design problems. Here, though, I have also noted that, where a stochastic environment prevails, we would need an infinite population to allow for a perfect picture of the causal contribution of individual traits purely by comparison. Obviously, this will not obtain in any real-world scenario.

Importantly though, these two forms of analysis – comparison and "engineering" – are not mutually exclusive and can, in fact, complement one another in making the same inferences. Engineering analyses might help us bridge the gaps where relevant comparisons are not available and vice versa, so that comparison might step in where we do not fully understand how systems function. Indeed, the two approaches might blend together in their application. For instance, an engineering analysis might be based on comparisons or analogies to similar systems. Thus, the central place foraging theory was derived not simply via abstract reasoning, but also via comparison of various bird species. Furthermore, it can also be applied by analogy to the behaviours of entirely disparate animals – for instance, in explaining the tree felling behaviours of beavers (Jenkins 1980).

Considering all this, it seems that there is definite scope for integration of my points on comparative populations with Bouchard and Rosenberg on ecological fitness and perhaps more broadly to similar literature around "engineering" style causal analyses in our reasoning about selection. The idea of comparative populations might also synthesise well with the counterfactual approach to selection taken by Huneman (2012), so there is ample scope for productive interaction with existing work.

6.2. Unification With Thermodynamic Approaches to Fitness and Life

The general theme here of assessing selection via comparison to a wider system is similar to my points in chapter five. There, I considered biological fitness as the extent to which entities are able to maintain or increase negentropy in the face of the system-wide decay predicted by the second law of thermodynamics. As noted there, this would require that we establish a baseline for the overall behaviour of the relevant system against which to compare the success of our focal entities.

This idea of establishing a background by which to judge success clearly echoes the role I have described here for comparative populations. As such, the comparative population idea might be developed to fulfil this role of establishing the background by which we establish the comparative performance of individuals or types within a thermodynamic frame. This outcome would be highly satisfying, as we would have unified our definition of life and our theory of biological fitness and provided a suitable population concept within the same overarching theoretical scheme. Thus, we would identify life as a characteristic "local inversion" of the second law of thermodynamics (as per

Schrödinger 1944) and assess fitness as a function of the magnitude and persistence of this characteristic behaviour relative to an appropriate comparison.

Conclusion

Despite the Darwinian population concept's importance, no pre-existing consensus definition existed. Indeed, researchers have gone about bounding their Darwinian populations in different ways, with confusion sometimes emerging as a result. With a paucity of explicit work on the Darwinian population, investigators presumably relied largely upon uninspected intuitions.

Beyond the continuing task of examining our assumptions around selection, this chapter was also necessary was to guard against my previous points on competition and fitness being undermined by conflicting Darwinian population concepts. An adverse, universally applied Darwinian population concept might simply negate much of my analysis in previous chapters.

I conducted a systematic analysis of possible criteria by which to delineate Darwinian populations. However, all the criteria examined came with significant problems; both in the details of how they might be developed and applied, and from examples where selection clearly proceeds without such criteria being realised.

With no prospect of a universal, singular Darwinian population concept, a pluralist approach as per Stegenga is required. That a strict, singular Darwinian population concept is untenable also means that my work in other chapters will not be undermined by an incompatible definition.

Starting from observed tensions in our intuitions around Darwinian populations, I went on to show that we often assemble groups of individuals in purely pragmatic fashion to support inferences about causation within instances of selection. I held that we then frequently mistake these "comparative populations" for causally meaningful Darwinian populations and thus try to find the relevant connections between members. In practice, comparative populations might indeed elide with the Darwinian variety, but the two groupings might also be highly divergent.

Finally, I made brief remarks on how this insight around comparative populations might be productively combined with the work of Bouchard and Rosenberg and Huneman on inference and counterfactual causation. The comparative population idea might also synthesise with my own thermodynamic take

on selection, allowing us to arrive at a combined account of life and biological fitness, replete with an appropriate population concept.

CONCLUSION

In this piece, I have systematically analysed a set of assumptions underlying conventional accounts of natural selection. To re-state, these were as follows:

1. *Competition is an inherent part of natural selection*
2. *Assessing fitness is a matter of counting some number of units*
3. *Fitness is manifested in an immediate, single-generation time frame*
4. *The population involved in a case of natural selection is self-evident*

Here, I will recap how the discussion in the preceding chapters has addressed these assumptions, before examining how this has changed our overall view of selection. Finally, I will assess whether, and to what extent, such change represents a constructive step for our understanding of natural selection.

1. Recapping the Discussion

To begin, it will be useful to briefly revisit the discussion across the preceding chapters:

Chapter One

Here, I showed that selection does not require competition (as per assumption one, above). Rather, I held that selection can be driven by other forms of interaction and can also proceed in the absence of any salient causal relations between participants at all. Thus, I set out a taxonomy of forms of selection, distinguishing parametric and strategic forms, and partitioning the latter category into competitive, cooperative and exploitative types. Contra Godfrey-Smith, I showed that competition is not a uniquely powerful driver of selection in terms of generating novel adaptation, but that selection driven by cooperative and exploitative interactions can more readily lead to the emergence of new adaptive traits.

Chapter Two

I noted that there were many apparent cases of selection where biological success is demonstrated not by increasing or sustaining the number of some set of entities (as per assumption two, above), but in terms of somatic size or longevity. Showing that these different fitness metrics could not be reduced to one another, I held that a pluralist approach to measuring fitness was essential to satisfactorily capture all cases of selection. I also noted that we were left with questions around how the different aspects of

fitness related to one another at a conceptual level and whether we might be able to derive a common currency between the different aspects of fitness identified. These questions were deferred until chapters four and five.

Chapter Three

Here, I effectively extended the arguments made in chapter two into the temporal dimension to challenge the assumption that fitness is manifested in a single-generation time frame (as per assumption three, above). I pointed to cases in the literature where biological success is manifested over longer periods of time and where maintaining a single-generation time frame would thus be misleading. Considering possible alternative approaches, I showed that assessing fitness at *any* single point in time, or via any single aggregating measurement, would inherently lead to a loss of biologically salient information. This led to my intra-case pluralist approach, such that we should permissively adopt different measurements of fitness over time; not only when dealing with different cases of selection, but also in understanding a single case. Whilst it meant all-time fitness rankings would not always be possible, I showed that this stance facilitated our understanding of how levels of biological success at different points in time depend upon, and are constrained by, one another.

Chapter Four

In chapter four, I returned to the discussion of fitness metrics which I began in chapter two. Seeking out a "common currency" fitness metric and a way to unite the different aspects of fitness conceptually, I noted that various authors have considered selection or evolution more generally in terms of energy or resource consumption. This approach promised to reconcile the aspects of fitness identified in that all the processes associated with them inherently require the input of energy and/or resources. I grouped these ideas together under the umbrella of "consumption accounts".

Van Valen's work provided the most directly relevant and fully developed attempts to consider fitness in terms of both resource and energy consumption. However, an analysis of Van Valen's work revealed fundamental problems, compromising not only his own but *any* similar consumption account. Specifically, I noted "efficiency" problems, where input of energy/resources will fail to track output in terms of biological success, as well as issues capturing selection amongst "non-metabolic" or non-living entities.

Chapter Five

Whilst consumption accounts ultimately proved unworkable, considering selection in terms of the basic physics involved did seem to get at some element of truth. Thus, in chapter five, I suggested a thermodynamic approach might enable us to unite our various fitness metrics, whilst avoiding the

problems associated with consumption accounts. This was to be accomplished by considering those aspects of fitness all as means of generating or sustaining negentropy. This took the idea from Schrödinger and others of defining life as a "local inversion" of the second law of thermodynamics and measured fitness effectively as the magnitude of that inversion.

Unfortunately, for any system complex enough to be interesting, we will not be able to generate negentropy-based fitness values in practice. However, the reduction to negentropy remained sound in principle. Thus, this thermodynamic approach succeeds in reconciling the various aspects of fitness at a conceptual level, explaining what valid metrics will have in common and granting them meaning where they are employed. Perhaps the more significant prize, though, is that this approach allows unification between our fitness concept and Schrödinger's definition of life. Thus, we might say that, where one organism is fitter than a peer, it is a more successful lifeform.

Chapter Six

Finally, I analysed the Darwinian population concept (addressing assumption four, above), showing that it is far from clear how we ought to bound the groups of entities regarded as undergoing selection together. Largely following Stegenga, I systematically ruled out all the commonly cited criteria by which we might bind such groupings and noted that this finding will necessitate adoption of a pluralist approach to identifying Darwinian populations in practice.

I also explored why Darwinian populations prove resistant to analysis and why we hold conflicting intuitions around them. Thus, I suggested we often conflate Darwinian populations with "comparative populations" – pragmatic groupings made to allow comparative inferences as to the causation underlying selection. Subsequently attempting to discover causal relationships between members where these might not exist at all confuses our understanding of Darwinian populations. I also noted that the comparative population idea might combine well with other authors' work on inference in selection and my thermodynamic approach to fitness.

2. Stepping Back – A Look at My General Findings

In short, none of the standard assumptions identified in the introduction have fully stood up to scrutiny. This has led to interesting conclusions in each chapter. However, we can also consider the aggregate impact of these findings on our overall picture of natural selection, as well as how this then affects our view of the assumptions we began with.

2.1. Selection Is a Broader Phenomenon Than Envisioned by Conventional Accounts

Whilst none of the four assumptions above stand up to analysis as genuine universals in selection, none have turned out to be "wrong" for all cases of selection. For instance, many cases of selection *are* competitive. Fitness *is* often manifested in terms of number of individuals, gene copies or similar and frequently *is* well-captured at a single-generation timescale. The Darwinian population *is* often fairly unambiguous.

None of our findings in the preceding chapters have served to contract the set of cases to which we might apply our theory of selection. Rather, the effect of my analysis in each area we have examined has been to increase the breadth of scenarios that we can coherently interpret as instances of selection. Thus, we can now perceive selection driven *not only* by competitive interactions but *also* by cooperative and exploitative relations and by interactions purely with the abiotic environment. We can account for fitness in terms of biomass and persistence over any time period *as well as* number of individuals after a single generation. We also now have a host of viable options for defining the Darwinian population. In short, by demonstrating that the standard assumptions do not hold universally, we have not thrown out cases of selection for which those assumptions *do indeed* hold.

We have thus emerged with a picture of natural selection as a much broader, more general phenomenon than before – with this corresponding to a significant increase in the explanatory scope of our theory. This has been accomplished without any significant loss of previous explanatory capacity. In this light, the standard assumptions identified can be thought of as defining a certain subset of cases to which conventional accounts of natural selection have been tailored.

2.2. Standard Assumptions Do Not Identify "Paradigm" Cases of Selection

Now, it is tempting to make the inferential step to the idea that the standard assumptions we have rejected in fact serve to identify a set of "paradigm" cases of natural selection. Thus, we might imagine that, where these assumptions *do* hold and selection *is* a function of competition amongst a readily defined group, where single-generation reproductive success tracks fitness, that this is selection in its "purest" form. In particular, as per Godfrey-Smith or Dawkins, we might speculate that this is a particularly powerful mode of selection in driving the emergence of novel adaptation.

However, my findings have not supported this stance. In particular, as discussed in chapter one, selection driven by cooperative or exploitative interactions offers a clearer route to the emergence of novel adaptation than does competition. Similarly, we have seen many clear examples where fitness in terms of biomass or persistence, and across non-standard timescales, seem to be the dominant factors

governing the adaptive evolution of real-world species. As such, we cannot rationally privilege the set of instances where these assumptions do hold as any kind of "paradigm" mode of selection.

2.3. Standard Assumptions Are a Reflection of Historical Focus

If the standard assumptions examined here do not define "paradigm" instances of selection, then we might wonder why they have been so persistent and have been challenged so little. In reality, the truth is not that these assumptions will hold in some exceptionally pure, "Platonic" form of selection, but rather that they will tend to hold in the cases of selection upon which biologists and theoreticians have historically focused.

Particularly, there has been an historical focus on selection occurring amongst the members of what I have referred to as "familiar" species. These are the kind of mid-sized, sexually reproducing, overall-physically-uniform kinds of organisms that humans engage with most typically in day-to-day life (and of which humans themselves are an example).

Amongst such "familiar" species, the assumptions above will indeed tend to hold true. Resource scarcity or competition for mates will often drive selection and we do not typically worry about how we define Darwinian populations because often (as noted in chapter six) all of the criteria we might apply generate the same grouping of individuals anyway. Most notably, the close similarity between members of these familiar species means that simply counting individual units over a single time period will be sufficient to reliably track biological success. The individuals of less-familiar species do not manifest as such conveniently standardised units, though – which is where we have typically seen our standard assumptions break down.

Thus, we can fairly safely assume that, within their own species, two humans, two cattle or two sparrows will be relatively close to equivalent in terms of variables like biomass or lifespan, and we can apply conventional accounts of selection when dealing with such species without much concern this will prove misleading. However, we cannot justify such an assumption of equivalence between members of other species, such as the individual groves of aspen or immortal jellyfish discussed in this piece. As a result, conventional approaches to selection will often mislead when applied to less-familiar forms of life. Indeed, throughout my discussion, something of a theme was evident as the standard assumptions underpinning conventional accounts of natural selection broke down when forced to account for the kinds of selective phenomena we encounter in less-familiar species.

That biological theory has been impeded by an historical tendency to focus on familiar species is already widely recognised and will not come as news to many readers. This bias within our theories would not

be quite so damaging if those species made up the overwhelming majority of biological forms. However, this is not the case at all. In fact, this grouping of familiar species represents a rather skewed sample of the natural world. A stock example of this kind of skew in theory is Mayr's (1942, 1963) still widely cited biological species concept (also discussed in chapter six), which functions admirably in familiar, sexually reproducing species, but breaks down in the face of the kind of asexual reproducers which account for the bulk of biological variety on Earth.

3. A Step Forward or a Step Back?

In the preceding chapters, a lot of time has been spent on taking apart our understanding of natural selection. Given this, one might then wonder if we are any further forward than where we began. Does the overall picture of natural selection which has emerged represent a step forward or a step back?

In particular, the general direction of travel in most of my arguments has been from a relatively simple, cut-and-dried theory to a more pluralist, ambiguous view. Thus, we have gone from an inherently competitive view of selection to having selection driven by the multiplicity of interactions described in chapter one. We have transitioned from the idea of fitness as a simple matter of counting individuals one generation hence, to a variety of incommensurable aspects of biological success, measured at an indefinite number of points in time. Finally, we have moved from scant consideration of an apparently clear-cut Darwinian population to a multifarious concept, liable to confusion with pragmatic inferential groupings.

Some readers might take these moves as a series of overall-retrograde steps. Traditionally, it has been the task of the theoretician to offer more elegant, parsimonious accounts of their target phenomena. Work is commended for having simplified or unified concepts, rather than decomposing and complexifying them, as I have arguably done with our ideas of competition, fitness and the Darwinian population.

However, I have not intended to put forward a wrecking account of selection. Where I have advocated for moves toward pluralist or similarly complexified accounts, it has typically been for the purpose of significantly expanding the explanatory scope of our theory of natural selection. By capturing nature more faithfully, we emerge with an account of selection which is more useful to us across a wider range of scenarios.

I have generally advocated for "pluralism-in-practice" in the subjects I have explored, holding that we might apply multiple fitness metrics at different points in time, with Darwinian populations defined via various criteria and in context of competition or otherwise. However, my approach does also offer unification at the conceptual level. Specifically, my thermodynamic approach to fitness offers the conceptual unification of the different aspects of fitness identified in chapter two, whilst further uniting our fitness concept with Schrödinger's popular thermodynamic definition of life. I also suggest that my comparative population idea might be linked back to the same thermodynamic approach. All this must surely go some way to balance more fragmented theory elsewhere.

Though I accept that talk of negative entropy in relation to fitness and selection is likely to seem somewhat eccentric to many readers, I note in chapter five that this approach picks up on ideas that have been expressed in various forms by many different authors long before Schrödinger's (1944) *What is Life?*, and which have only gained increased traction since. In this light, the conceptually useful but esoteric language of thermodynamics unfortunately serves to conceal that my approach to selection is largely a re-statement of older and fairly commonplace ideas.

In final summation, then, this piece has hopefully delivered a productive analysis of several foundational concepts of our theory of natural selection, as well as proposing a wider framework with which to underpin and crosslink those concepts, and indicating directions for further research. With further development, the approach to selection I have taken here might eventually form the basis for a new schematic statement of the fundamental character of natural selection – akin to Lewontin's heritable variation of fitness criteria or Brandon's PNS. However, my overall move towards a more general, pluralist approach will likely make such a restatement quite different in character to its predecessors.

BIBLIOGRAPHY

Alcock, J., 1994. Postinsemination associations between males and females in insects: the mate-guarding hypothesis. *Annual Review of Entomology*, *39*(1), pp.1-21.

Andersson, M., 1982. Female choice selects for extreme tail length in a widowbird. *Nature*, *299*(5886), pp.818-820.

Ayala, F.J. and Campbell, C.A., 1974. Frequency-dependent selection. *Annual Review of Ecology and Systematics*, *5*(1), pp.115-138.

Azua-Bustos, A. and Vega-Martínez, C., 2013. The potential for detecting 'life as we don't know it' by fractal complexity analysis. *International Journal of Astrobiology, 12*(4), pp.314-320.

Bar-On, Y.M., Phillips, R. and Milo, R., 2018. The biomass distribution on Earth. *Proceedings of the National Academy of Sciences*, *115*(25), pp.6506-6511.

Beatty, J. and Finsen, S., 1989. Rethinking the propensity interpretation: A peek inside Pandora's box. In Ruse, M. (ed), *What the Philosophy of Biology is*. Dordrecht, Springer, pp.17-30.

Bernstein, H., Byerly, H.C., Hopf, F.A., Michod, R.A. and Vemulapalli, G.K., 1983. The Darwinian dynamic. *The Quarterly Review of Biology*, *58*(2), pp.185-207.

Birch, J., 2016. Natural selection and the maximization of fitness. *Biological Reviews*, 91 (3). pp.712-727.

Brandon, R., 1990. *Adaptation and Environment*. Princeton, NJ, Princeton University Press.

Brandon, R., 2014. Natural Selection. In Zalta, E.N. (ed.), *The Stanford Encyclopedia of Philosophy* (Spring 2014 Edition), URL = <https://plato.stanford.edu/archives/spr2014/entries/natural-selection/>.

Brillouin, L., 1949. Life, thermodynamics, and cybernetics. *American Scientist*, *37*(4), pp.554-568.

Brisson, D., 2018. Negative frequency-dependent selection is frequently confounding. *Frontiers in Ecology and Evolution*, *6*, p. 10.

Bryant, D.M. and Turner, A.K., 1982. Central place foraging by swallows (Hirundinidae): the question of load size. *Animal Behaviour*, *30*(3), pp.845-856.

Boltzmann, L., 1886. Der Zweite Hauptsatz der Mechanischen Waermetheorie, (The Second Principle of the Mechanical Theory of Heat). *Akademie der Wissenschaften*, 36, pp.225-259.

Boomsma, D., Busjahn, A. and Peltonen, L., 2002. Classical twin studies and beyond. *Nature Reviews Genetics*, *3*(11), pp.872-882.

Bouchard, F., 2008. Causal processes, fitness, and the differential persistence of lineages. *Philosophy of Science*, *75*(5), pp.560-570.

Bouchard, F., 2011. Darwinism without populations: A more inclusive understanding of the "Survival of the Fittest". *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, *42*(1), pp.106-114.

Bouchard, F. and Rosenberg, A., 2004. Fitness, probability and the principles of natural selection. *The British Journal for the Philosophy of Science*, *55*(4), pp.693-712.

Brodribb, T.J., Pittermann, J. and Coomes, D.A., 2012. Elegance versus speed: Examining the competition between conifer and angiosperm trees. *International Journal of Plant Sciences*, *173*(6), pp.673-694.

Burger, J.R., George Jr, M.A., Leadbetter, C. and Shaikh, F., 2019. The allometry of brain size in mammals. *Journal of Mammalogy*, *100*(2), pp.276-283.

Cain, A.J. and Sheppard, P.M., 1954. Natural selection in Cepaea. *Genetics*, *39*(1), p.89.

Carroll, L., 1872. *Through the Looking-Glass, and What Alice Found There*. London, MacMillan.

Casselman, A., 2007. Strange but true: the largest organism on earth is a fungus. *Scientific American*, URL = <https://www.scientificamerican.com/article/strange-but-true-largest-organism-is-fungus/>.

Chaisson, E.J., 2009. Exobiology and Complexity. In Meyers R. (ed) *Encyclopedia of Complexity and Systems Science*. New York, Springer, pp.3267-3284.

Chaisson, E.J., 2011. Energy rate density as a complexity metric and evolutionary driver. *Complexity*, *16*(3), pp.27-40.

Clarke, E., 2010. The Problem of Biological Individuality. *Biological Theory*, *5*(4), pp.312-325.

Clarke, E., 2011. Plant Individuality and Multilevel Selection Theory. In Sterelny, K. and Calcott, B. (eds.), *The Major Transitions in Evolution Revisited*. Cambridge, MA, MIT Press, pp.227-250.

Clarke, E., 2012. Plant individuality: A solution to the demographer's dilemma. *Biology & Philosophy*, *27*(3), pp.321-361.

Clout, M.N. and Lowe, S.J., 2000. Invasive species and environmental changes in New Zealand. *Invasive Species in a Changing World*, pp.369-383

Cooper, W.S., 1984. Expected time to extinction and the concept of fundamental fitness. *Journal of Theoretical Biology*, *107*(4), pp.603-629.

Corning, P.A. and Kline, S.J., 1998. Thermodynamics, information and life revisited, Part I: 'To be or entropy'. *Systems Research and Behavioral Science: The Official Journal of the International Federation for Systems Research*, *15*(4), pp.273-295.

Davies, N.B., Krebs, J.R., 1993. *An Introduction to Behavioural Ecology*. Oxford, Blackwell.

Dawkins, R.,1976. *The Selfish Gene*. Oxford, Oxford University Press. (Specific page references have been made to the 2016 edition, listed below)

Dawkins, R., 1982. *The Extended Phenotype: The Gene as the Unit of Selection*. Oxford, Oxford University Press.

Dawkins, R., 1986. *The Blind Watchmaker*. Harlow, Longman Scientific and Technical.

Dawkins, R., 2016. *The Selfish Gene: 40th Anniversary Edition*. Oxford, Oxford University Press.

Doebeli, M. and Dieckmann, U., 2000. Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *The American Naturalist*, *156*(S4), pp.S77-S101.

Doolittle, W.F., 2014. Natural selection through survival alone, and the possibility of Gaia. *Biology & Philosophy*, *29*(3), pp.415-423.

Dybas, H.S. and Lloyd, M., 1974. The habitats of 17-year periodical cicadas (Homoptera: Cicadidae: Magicicada spp.). *Ecological Monographs*, *44*(3), pp.279-324.

Editors of the Encyclopaedia Britannica, 2020. Natural Selection. *Encyclopædia Britannica*, URL = <https://www.britannica.com/science/natural-selection>.

Edwards, A.W., 1998. Natural selection and the sex ratio: Fisher's sources. *The American Naturalist*, *151*(6), pp.564-569.

Elton, C.S., 1927. *Animal Ecology*. London, Sidgwick and Jackson.

Elton, C. and Nicholson, M., 1942. The ten-year cycle in numbers of the lynx in Canada. *The Journal of Animal Ecology*, pp.215-244.

Ehrenfest, P. and T., 1911. The Conceptual Foundations of the Statistical Approach in Mechanics. *Mechanics Enziklopädie der Mathematischen Wissenschaften*.

Endler, J., 1986. *Natural Selection in the Wild*. Princeton, Princeton University Press.

Ereshefsky, Marc, "Species". In Zalta, E.N. (ed.), *The Stanford Encyclopedia of Philosophy* (Fall 2017 Edition), URL = <https://plato.stanford.edu/archives/fall2017/entries/species/>.

Fisher, R. A., 1930. *The Genetical Theory of Natural Selection*. Oxford, Clarendon.

Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D. and Holle, B.V., 2007. The invasion paradox: Reconciling pattern and process in species invasions. *Ecology*, *88*(1), pp.3-17.

Futuyma, D.J., 1976. *Evolutionary Biology*. Sunderland, Sinauer.

Gannett, L., 2003. Making populations: Bounding genes in space and in time. *Philosophy of Science, 70*(5), pp.989-1001.

Gardner, A., 2008. The Price equation. *Current Biology, 18*(5), pp.R198-R202.

Gillespie, J.H., 1977. Natural selection for variances in offspring numbers: A new evolutionary principle. *American Naturalist*, 111, pp1010–1014.

Gilpin, M.E., 1973. Do hares eat lynx?. *The American Naturalist, 107*(957), pp.727-730.

Ghiselin, M.T., 1974. A radical solution to the species problem. *Systematic Biology, 23*(4), pp.536-544.

Gill, D.E. and Halverson, T.G., 1984. Fitness variation among branches within trees. In Shorrocks, B. (ed.), *Evolutionary Ecology: The 23rd Symposium of the British Ecological Society, Leeds, 1982*. Oxford, Blackwell, pp. 105–116.

Glymour, B., 1999. Is pure R-selection really selection?. *Philosophy of Science, 66*, pp.S185-S195.

Glymour, B., 2001. Selection, indeterminism, and evolutionary theory. *Philosophy of Science, 68*(4), pp.518-535.

Godfrey Smith, P., 2009. *Darwinian Populations and Natural Selection*. Oxford, Oxford University Press.

Godfrey-Smith, P., 2014. *Philosophy of Biology*. Princeton, Princeton University press.

Godman, M., 2018. Scientific realism with historical essences: The case of species. *Synthese*, pp.1-17.

Gorban, A.N., 2006. Basic types of coarse-graining. In Gorban, A.N., Kazantzis, N.K., Kevrekidis, I.G., Öttinger, H.C. and Theodoropoulos, C. (eds.), *Model reduction and coarse-graining approaches for multiscale phenomena*. Berlin, Heidelberg, Springer, pp.117-176.

Gould, S. J., 1989. *Wonderful Life*. New York, Norton.

Grafen, A., 1999. Formal Darwinism, the individual–as–maximizing–agent analogy and bet–hedging. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*(1421), 799-803.

Grafen, A., 2006. A theory of Fisher's reproductive value. *Journal of Mathematical Biology*, *53*(1), pp.15-60.

Grafen, A., 2014. The formal Darwinism project in outline. *Biology & Philosophy*, *29*(2), pp.155-174.

Guidetti, R., Altiero, T. and Rebecchi, L., 2011. On dormancy strategies in tardigrades. *Journal of Insect Physiology*, *57*(5), pp.567-576.

Harper, J.L. 1977. *Population biology of plants*. London, Academic Press.

Hamilton, W.D., 1964. The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, 7(1).

Hoffmann, B.D. and Broadhurst, L.M., 2016. The economic cost of managing invasive species in Australia. *NeoBiota*, *31*, p.1.

Hoso, M., Asami, T. and Hori, M., 2007. Right-handed snakes: Convergent evolution of asymmetry for functional specialization. *Biology Letters*, *3*(2), pp.169-173.

Houge, G., Bruland, O., Bjørnevoll, I., Hayden, M.R. and Semaka, A., 2013. De novo Huntington disease caused by 26–44 CAG repeat expansion on a low-risk haplotype. *Neurology*, *81*(12), pp.1099-1100.

Hull, D.L., 1980. Individuality and selection. *Annual Review of Ecology and Systematics*, *11*(1), pp.311-332.

Hull, David L., 1988. *Science as a Process: An Evolutionary Account of the Social and Conceptual Development of Science*. Chicago, University of Chicago Press.

Huneman, P., 2012. Natural selection: A case for the counterfactual approach. *Erkenntnis*, *76*(2), pp.171-194.

Illarioshkin, S.N., Klyushnikov, S.A., Vigont, V.A., Seliverstov, Y.A. and Kaznacheyeva, E.V., 2018. Molecular pathogenesis in Huntington's disease. *Biochemistry (Moscow)*, *83*(9), pp.1030-1039.

Ito, H., Kakishima, S., Uehara, T., Morita, S., Koyama, T., Sota, T., Cooley, J.R. and Yoshimura, J., 2015. Evolution of periodicity in periodical cicadas. *Scientific Reports*, *5*, p.14094.

Jantsch, E., 1980. *The Self-Organizing Universe: Scientific and Human Implications of the Emerging Paradigm of Evolution*. New York, Pergamon.

Janzen, D.H., 1977. What are dandelions and aphids?. *The American Naturalist*, *111*(979), pp.586-589.

Jenkins, S.H., 1980. A size-distance relation in food selection by beavers. *Ecology*, *61*(4), pp.740-746.

Jeuken, M., 1975. The biological and philosophical definitions of life. *Acta Biotheoretica*, *24*(1-2), pp.14-21.

Kettlewell, H.B.D., 1955. Selection experiments on industrial melanism in the Lepidoptera. *Heredity*, *9*(3), pp.323-342.

Klingenberg, C.P., 2008. Morphological integration and developmental modularity. *Annual Review of Ecology, Evolution, and Systematics*, *39*, pp.115-132.

Krimbas, C.B., 2004. On fitness. *Biology and Philosophy*, *19*(2), pp.185-203.

Kojima, K.I., 1971. Is there a constant fitness value for a given genotype? NO!. *Evolution*, *25*(2), pp.281-285.

Kojima, T., 1951. On the brain of the sperm whale (Physeter catodon L.). *Scientific Reports of the Whales Research Institute Tokyo*, *6*, pp.49-72.

Kuhn, T., 1962. *The Structure of Scientific Revolutions*. Chicago, University of Chicago Press.

Lack, D., 1947. The significance of clutch-size. *Ibis*, 89, pp.302-352.

Lack, D., 1948. The significance of clutch size. *Ibis*, 90, pp.25-45.

Lack, D., 1954. *The Natural Regulation of Animal Numbers*. Oxford, Clarendon.

Lennox, J.G. and Wilson, B.E., 1994. Natural selection and the struggle for existence. *Studies in History and Philosophy of Science Part A*, *25*(1), pp.65-80.

Lewens, T., 2004. *Organisms and Artifacts*. Cambridge, MA, MIT Press.

Lewens, T., 2007. *Darwin*. London, Routledge.

Lewens, T., 2010. Natural selection then and now. *Biological Reviews*, *85*(4), pp.829-835.

Lewens, T., 2012. Pheneticism reconsidered. *Biology & Philosophy*, *27*(2), pp.159-177.

Lewens, T., 2015. The nature of philosophy and the philosophy of nature. *Biology & Philosophy*, *30*(4), pp.587-596.

Lewens, T., 2018. Cultural Evolution. In Zalta, E.N. (ed.), *The Stanford Encyclopedia of Philosophy* (Summer 2018 Edition), URL = <https://plato.stanford.edu/archives/sum2018/entries/evolution-cultural/>.

Lewis, D., 1973. *Counterfactuals*. Oxford, Blackwell.

Lewis, G.N. and Randall, M., 1923. *Thermodynamics and the Free Energy of Chemical Substances*. New York, McGraw-Hill.

Lewontin, R.C., 1970. The units of selection. *Annual Review of Ecology and Systematics*, *1*(1), pp.1-18.

Lloyd, E., 2020. Units and Levels of Selection. In Zalta, E.N. (ed.), *The Stanford Encyclopedia of Philosophy* (Spring 2020 Edition), URL = <https://plato.stanford.edu/archives/spr2020/entries/selection-units/>.

Lloyd, M. and Dybas, H.S., 1966(a). The periodical cicada problem. I. Population ecology. *Evolution*, *20*(2), pp.133-149.

Lloyd, M. and Dybas, H.S., 1966(b). The periodical cicada problem. II. Evolution. *Evolution*, *20*(4), pp.466-505.

Lotka, A.J., 1922(a). Contribution to the energetics of evolution. *Proceedings of the National Academy of Sciences of the United States of America*, *8*(6), p.147.

Lotka, A.J., 1922(b). Natural selection as a physical principle. *Proceedings of the National Academy of Sciences of the United States of America*, *8*(6), p.151.

Lotka, A.J., 1944. Evolution and thermodynamics. *Science & Society*, pp.161-171.

Lotka, A.J., 1945. The law of evolution as a maximal principle. *Human Biology*, *17*(3), pp.167-194.

McShea, D.W., 1998. Possible largest-scale trends in organismal evolution: Eight "live hypotheses". *Annual Review of Ecology and Systematics*, *29*(1), pp.293-318.

MacArthur, R.H. and Wilson, E.O., 1967. *Island Biogeography*. Princeton, Princeton University Press.

MacLulich, D.A., 1937. Fluctuations in the numbers of the varying hare (*Lepus americanus*). *University of Toronto Studies Biological Series*, *43*, pp.1-136.

Marasco, A., Picucci, A. and Romano, A., 2016. Market share dynamics using Lotka–Volterra models. *Technological Forecasting and Social Change*, *105*, pp.49-62.

Marsh, C., 2013. Introduction to continuous entropy. *Department of Computer Science, Princeton University*.

Maturana, H. and Varela, F., 1973. *Autopoiesis: The Organization of the Living*. Dordrecht, Reidel

Maturana, H., and Varela, F., 1980. *Autopoiesis and Cognition: The Realization of the Living*. Dordrecht, Reidel.

Mayr, E., 1996. What is a species, and what is not?. *Philosophy of science*, *63*(2), pp.262-277.

Mayr, E., 1963. *Animal Species and Evolution*. Cambridge, MA, Harvard University Press.

Meinesz, A., Benichou, L., Blachier, J., Komatsu, T., Lemée, R., Molenaar, H., & Mari, X., 1995. Variations in the Structure, Morphology and Biomass of Caulerpa taxifolia in the Mediterranean Sea. *Botanica Marina*, *38*(1-6), pp.499-508.

Mills, S.K. and Beatty, J.H., 1979. The propensity interpretation of fitness. *Philosophy of Science*, *46*(2), pp.263-286.

Millstein, R.L., 2009. Populations as individuals. *Biological Theory*, *4*(3), pp.267-273.

Moser, D., Lenzner, B., Weigelt, P., Dawson, W., Kreft, H., Pergl, J., Pyšek, P., van Kleunen, M., Winter, M., Capinha, C. and Cassey, P., 2018. Remoteness promotes biological invasions on islands worldwide. *Proceedings of the National Academy of Sciences*, *115*(37), pp.9270-9275.

Nanay, B., 2005. Can cumulative selection explain adaptation?. *Philosophy of Science*, *72*(5), pp.1099-1112.

Nanay, B., 2010. Natural selection and the limitations of environmental resources. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, *41*(4), pp.418-419.

Nanay, B., 2011. Replication without replicators. *Synthese*, *179*(3), pp.455-477.

Neander, K., 1995(a). Pruning the tree of life. *The British Journal for the Philosophy of Science*, *46*(1), pp.59-80.

Neander, K., 1995(b). Explaining complex adaptations: A reply to Sober's' reply to Neander'. *The British Journal for the Philosophy of Science*, *46*(4), pp.583-587.

Neander, K., 1988. What does natural selection explain? Correction to Sober. *Philosophy of Science*, *55*(3), pp.422-426.

Odum, H.T. and Pinkerton, R.C., 1955. Time's speed regulator: The optimum efficiency for maximum power output in physical and biological systems. *American Scientist*, *43*(2), pp.331-343.

Orians, G.H. and Pearson, N.E., 1979. On the theory of central place foraging. In Horn, D.J., Mitchell, R.D. and Stairs, G.R. (eds.) *Analysis of Ecological Systems*. Columbus, OH, Ohio State University Press, pp.155-177.

Orr, H.A., 2009. Fitness and its role in evolutionary genetics. *Nature Reviews Genetics*, *10*(8), pp.531-539.

Okasha, S., 2003. Does the concept of “clade selection” make sense?. *Philosophy of Science*, *70*(4), pp.739-751.

Owen, D.F., 1966. Polymorphism in Pleistocene land snails. *Science*, *152*(3718), pp.71-72.

Pianka, E.R., 1970. On r-and K-selection. *The American Naturalist*, *104*(940), pp.592-597.

Piraino, S., Boero, F., Aeschbach, B., & Schmid, V., 1996. Reversing the Life Cycle: Medusae Transforming into Polyps and Cell Transdifferentiation in Turritopsis nutricula (Cnidaria, Hydrozoa). *Biological Bulletin*, *190*(3), pp.302-312.

Price, G.R., 1970. Selection and covariance. *Nature, 227*, pp.520–521.

Perutz, M.F., 1987. Physics and the riddle of life. *Nature, 32*, pp.555-558.

Pringle, R.M., 2005. The origins of the Nile perch in Lake Victoria. *BioScience*, *55*(9), pp.780-787.

Regan, C.T., 1925. Dwarfed males parasitic on the females in oceanic angler-fishes (Pediculati ceratioidea). *Proceedings of the Royal Society of London. Series B, Containing Papers of a Biological Character*, *97*(684), pp.386-400.

Reinhold, K., 2000. Maintenance of a genetic polymorphism by fluctuating selection on sex-limited traits. *Journal of Evolutionary Biology*, *13*(6), pp.1009-1014.

Reznick, D., Bryant, M.J. and Bashey, F., 2002. r-and K-selection revisited: the role of population regulation in life-history evolution. *Ecology*, *83*(6), pp.1509-1520.

Richardson, D.M. and Pyšek, P., 2007. Elton, CS 1958: The ecology of invasions by animals and plants. London: Methuen. *Progress in Physical Geography*, *31*(6), pp.659-666.

Rico-Gray, V. and Oliveira, P.S., 2007. *The ecology and evolution of ant-plant interactions*. Chicago, University of Chicago Press.

Ridley, M., 1996. *Evolution: Second Edition*. Cambridge, MA, Blackwell Science.

Rosenberg, A. and Bouchard, F., 2015. Fitness. In Zalta, E.N. (ed.), *The Stanford Encyclopedia of Philosophy* (Fall 2015 Edition), URL = <https://plato.stanford.edu/archives/fall2015/entries/fitness/>.

Ruse, M., 1971. Natural Selection in" The Origin of Species". *History and Philosophy of Science*, 1(4), pp.311-351.

Russell, B., 1927. *An Outline of Philosophy*. London, George Allen and Unwin.

Sæther, B.E. and Engen, S., 2015. The concept of fitness in fluctuating environments. *Trends in Ecology & Evolution*, *30*(5), pp.273-281.

Schneider, E.D, Kay, J.J., 1995. Order from Disorder: The Thermodynamics of Complexity in Biology. In Murphy, M.P. and O'Neill, L.A.J. (eds). *What is Life: The Next Fifty Years. Reflections on the Future of Biology*. Cambridge. Cambridge University Press, pp.161-172.

Schoener, T.W., 1979. Generality of the size-distance relation in models of optimal feeding. *The American Naturalist*, *114*(6), pp.902-914.

Schrödinger, E., 1944. *What is Life? The Physical Aspect of the Living Cell*. Cambridge, Cambridge University Press.

Shorter, J., 2010. Emergence and natural selection of drug-resistant prions. *Molecular Biosystems*, *6*(7), pp.1115-1130.

Siepielski, A.M., DiBattista, J.D., Evans, J.A. and Carlson, S.M., 2011. Differences in the temporal dynamics of phenotypic selection among fitness components in the wild. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1711), pp.1572-1580.

Sinervo, B. and Lively, C.M., 1996. The rock–paper–scissors game and the evolution of alternative male strategies. *Nature*, *380*(6571), pp.240-243.

Skagen, S.K., 1988. Asynchronous hatching and food limitation: A test of Lack's hypothesis. *The Auk*, *105*(1), pp.78-88.

Sober, E., 1980. Evolution, population thinking, and essentialism. *Philosophy of Science*, *47*(3), pp.350-383.

Sober, E., 1984. *The Nature of Selection: Evolutionary Theory in Philosophical Focus*. Cambridge, MA, MIT Press.

Sober, E., 1995. Natural selection and distributive explanation: A reply to Neander. *The British journal for the philosophy of science*, *46*(3), pp.384-397.

Sober, E., 2001. The Two Faces of Fitness. In Singh, R.S., Krimbas, C.B., Paul, D.B. and Beatty, J. (eds.), *Thinking about Evolution: Historical, Philosophical, and Political Perspectives*. Cambridge, Cambridge University Press.

Stegenga, J., 2016. Population Pluralism and Natural Selection. *The British Journal for the Philosophy of Science*, *67*(1), pp.1-29.

Sterelny, K. and Turney, J., 2007. *Dawkins vs. Gould: Survival of the fittest*. Cambridge, Icon Books.

Sterelny, K., 2009. Philosophy of Evolutionary Thought. In Ruse, M. and Travis, J. (eds.), *Evolution: The First Four Billion Years*. Cambridge, MA, Harvard University Press.

Stigall, A.L., 2012. Speciation collapse and invasive species dynamics during the Late Devonian "Mass Extinction". *GSA Today*, *22*(1), pp.4-9.

Tebbich, S., Sterelny, K. and Teschke, I., 2010. The tale of the finch: adaptive radiation and behavioural flexibility. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1543), pp.1099-1109.

Ticehurst, C.B., 1938. A Systematic Review of the Genus *Phylloscopus*. *London, British Museum*, p.1.

Tinbergen, L., 1960. The natural control of insects in pinewoods. *Archives Neerlandaises de Zoologie*, *13*(3), pp.265-343.

Thoday, J.M., 1953. Components of fitness. *Symposium for the Society for Experimental Biology*, 7(96), pp.113.

Thoday, J.M., 1958. Natural selection and biological process. In Barnett, S. (ed.) *A Century of Darwin*. London, Heinemann, pp.313–33.

Thornhill, R. and Alcock, J., 1983. *The Evolution of Insect Mating Systems*. Cambridge MA, Harvard University Press.

Toubiana, W. and Khila, A., 2019. Fluctuating selection strength and intense male competition underlie variation and exaggeration of a water strider's male weapon. *Proceedings of the Royal Society B*, *286*(1901), p.20182400.

Turner, G.F., 2007. Adaptive radiation of cichlid fish. *Current Biology*, *17*(19), pp.R827-R831.

Turner, J.S., 2009. *The Tinkerer's Accomplice*. Cambridge MA, Harvard University Press.

Van Valen, L.M., 1973. A new evolutionary law. *Evolutionary Theory*, *1*, pp.1-30.

Van Valen, L.M., 1975. Life, death, and energy of a tree. *Biotropica*, pp.259-269.

Van Valen, L.M., 1976. Energy and evolution. *Evolutionary Theory*, *1*, pp.179–229.

Van Valen, L.M., 1989. Three paradigms of evolution. *Evolutionary Theory*, *9*, pp.1–17.

Varela, F.G., Maturana, H.R. and Uribe, R., 1974. Autopoiesis: The organization of living systems, its characterization and a model. *Biosystems*, *5*(4), pp.187-196.

Vollrath, F., 1998. Dwarf males. *Trends in Ecology & Evolution*, *13*(4), pp.159-163.

Wagner, G.P. and Altenberg, L., 1996. Perspective: Complex adaptations and the evolution of evolvability. *Evolution*, *50*(3), pp.967-976.

Walsh, D.M., 1998. The scope of selection: Sober and Neander on what natural selection explains. *Australasian Journal of Philosophy*, *76*(2), pp.250-264.

Weatherson, B., 2016. David Lewis. In Zalta, E. N. (ed.), *The Stanford Encyclopedia of Philosophy* (Winter 2016 Edition), URL = <https://plato.stanford.edu/archives/win2016/entries/david-lewis/>.

Weber, B., 2018. Life. In Zalta, E.N. (ed.), *The Stanford Encyclopedia of Philosophy* (Summer 2018 Edition), URL = <https://plato.stanford.edu/archives/sum2018/entries/life/>.

Wehrl, A., 1991. The many facets of entropy. *Reports on Mathematical Physics*, *30*(1), pp.119-129.

Weissmann, C., 2012. Mutation and selection of prions. *PLoS Pathogens*, *8*(3), p.e1002582.

Wells, J.V. and Richmond, M.E., 1995. Populations, metapopulations, and species populations: What are they and who should care?. *Wildlife Society Bulletin (1973-2006)*, *23*(3), pp.458-462.

Wicken, J.S., 1980. A thermodynamic theory of evolution. *Journal of Theoretical Biology*, *87*(1), pp.9-23.

Wicken, J.S., 1986. Entropy and evolution: Ground rules for discourse. *Systematic Biology*, *35*(1), pp.22-36.

Williams, M.B., 1970. Deducing the consequences of evolution: A mathematical model. *Journal of Theoretical Biology*, *29*(3), pp.343-385.

Williams, K.S. and Simon, C., 1995. The ecology, behavior, and evolution of periodical cicadas. *Annual Review of Entomology*, *40*(1), pp.269-295.

Wilson, R.A. and Barker, M.J., 2019. Biological Individuals. In Zalta, E.N. (ed.), *The Stanford Encyclopedia of Philosophy* (Fall 2019 Edition), URL = <https://plato.stanford.edu/archives/fall2019/entries/biology-individual/>.

Wittmann, M.J., Bergland, A.O., Feldman, M.W., Schmidt, P.S. and Petrov, D.A., 2017. Seasonally fluctuating selection can maintain polymorphism at many loci via segregation lift. *Proceedings of the National Academy of Sciences*, *114*(46), pp.E9932-E9941.

Wright, S. and Dobzhansky, T., 1946. Genetics of natural populations. XII. Experimental reproduction of some of the changes caused by natural selection in certain populations of Drosophila pseudoobscura. *Genetics*, *31*(2), p.125.

Yamamura, N., 1986. An evolutionarily stable strategy (ESS) model of postcopulatory guarding in insects. *Theoretical Population Biology*, *29*(3), pp.438-455.

Yoshimura, J., 1997. The evolutionary origins of periodical cicadas during ice ages. *The American Naturalist*, *149*(1), pp.112-124.

Zamudio, K.R. and Sinervo, B., 2000. Polygyny, mate-guarding, and posthumous fertilization as alternative male mating strategies. *Proceedings of the National Academy of Sciences*, *97*(26), pp.14427-14432.